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PAR
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VARIATIONS INDIVIDUELLES DANS LA DISTRIBUTION SPATIALE ET L'ALIMENTATION DE L'OMBLE DE FONTAINE, *SALVELINUS FONTINALIS*, VIVANT DANS LES LACS DU BOUCLIER LAURENTIEN.

JUILLET 1996

AVANT-PROPOS

Suite aux réformes effectuées en septembre 1991, concernant les exigences à l'obtention du diplôme de 2e cycle en Sciences de l'environnement, les étudiants peuvent maintenant présenter leurs résultats sous forme d'articles scientifiques plutôt que sous forme d'un mémoire, comme il était obligatoire par le passé.

Il a été convenu avec mon directeur de recherche, le professeur Pierre Magnan, que trois articles issus de mon projet seraient soumis à des revues scientifiques (chapitre 1, 2 et 3). Ce mémoire comprend aussi la problématique présentée lors de la remise du protocole de recherche en avril 1994, une revue de littérature à jour sur le sujet, ainsi qu'une conclusion générale. Les trois articles ont été rédigés en anglais, mais un résumé substantiel en français de chacun d'eux est présenté en annexe.

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INTRODUCTION GÉNÉRALE

PROBLÉMATIQUE

La dynamique des populations animales est fonction des interactions qu'il y a entre les individus et leur habitat (Roese et al. 1991). Cependant, la variation individuelle à l'intérieur d'une même population a traditionnellement été ignorée parce qu'elle était considérée comme du "bruit" ou comme une déviation autour d'une réponse optimale (Lomnicki 1988, Ehlinger 1990). Ce n'est que récemment que des études ont commencé à considérer les conséquences adaptatives de la variation individuelle ainsi que sa portée sur la dynamique des populations (Ringler 1982, Lomnicki 1988, Ehlinger 1990, Roese et al. 1991, Zebra et Collins 1992). Par exemple, la variation individuelle, à cause de son effet sur la répartition des ressources alimentaires entre les membres d'une population, doit permettre de maintenir une population à un niveau plus dense et dans un état plus stable que ce qui pourrait être maintenu autrement (Ringler 1982, Lomnicki 1988).

Trois questions importantes sont à considérer dans l'étude des variations individuelles (Lomnicki 1988): (1) quelle est la structure de la variation individuelle à l'intérieur d'une population, pour un paramètre donné? (2) quels sont les mécanismes responsables de cette variation? et (3) quelles sont les conséquences de cette variation individuelle sur les modèles existants (dynamique des populations, répartition des ressources, sélection des proies)?

Chez les poissons, les études du comportement alimentaire et de la sélection de l'habitat ont mis l'emphase soit sur les "réponses moyennes" au niveau de la population (écologie classique), soit sur les réponses au niveau des individus (éthologie). Dans les deux cas, la variation individuelle était généralement considérée comme du "bruit" relié à la nature de l'environnement, des individus ou des méthodes employées (Ehlinger 1990).

Notre projet de recherche vise à faire ce lien entre l'écologie classique et l'éthologie en posant les trois questions énumérées ci-haut (Lomnicki 1988), où les paramètres étudiés seront la distribution spatiale et l'alimentation de l'Omble de fontaine[1].

REVUE DE LITTÉRATURE

Description et utilisation du système de radio-télémétrie

La biotélémétrie aquatique est un outil précieux pour l'étude du mouvement, du comportement, des conditions ambiantes et de certaines fonctions physiologiques des animaux sous l'eau. Dans de telles études, les données sont obtenues par voie de signaux provenant d'un émetteur placé sur ou dans l'animal. Les premiers systèmes utilisaient les signaux ultrasoniques, alors que récemment, l'usage de signaux radiophoniques a fait son apparition (Stasko et Pincock 1977).

Les avantages des systèmes radiophoniques par rapport aux systèmes ultrasoniques sont si importants que Stasko et Pincock (1977) suggèrent que l'utilisation des ultrasons devrait se limiter aux situations où les premiers ne peuvent être utilisés. La principale limite des ondes radios vient de leur grande atténuation dans l'eau. Cette atténuation devient très importante en eau salée ou en eau douce de forte conductivité. En contre-partie, l'eau douce de faible conductivité permet l'usage d'un tel système. Le signal capté provient de l'émergence de celui-ci directement au-dessus de l'animal, avant de couvrir la distance le séparant du récepteur par la voie des airs. Ceci n'est pas un problème dans la plupart des situations, c'est-à-dire dans les ruisseaux ou les lacs peu profonds, où l'animal est rarement situé à plus de quelques mètres de la surface (Salomon 1982). Les principaux avantages des

[1]L'emploi de la majuscule pour les noms d'espèces est en accord avec la recommandation de Chabot et David (1986).

consommation énergétique, donc durée de vie plus longue de l'émetteur; (2) très peu d'interférences des bruits ambiants; (3) détection possible sur des distances considérables dans l'air (Salomon 1982); (4) l'élément de réception (antenne) peut être à l'extérieur de l'eau; (5) réception possible malgré une eau recouverte d'algues ou de glace (McCleave, Power et Rommel 1978).

Utilisation et effet de l'utilisation d'appareils de télémétrie chez les poissons

Jusqu'à maintenant, un certain nombre d'études sur le comportement et la biologie des poissons ont nécessité l'utilisation de systèmes de télémétrie. Dans la plupart des cas, ces études portent sur les déplacements des poissons, et plus particulièrement sur le comportement de retour au gîte (angl. : homing) chez le saumon (McCleave et Power 1978, Ruggerone et Thomas 1990, Ogura et Ishida 1992). Ces études ont aussi porté sur la vitesse de déplacement et les températures et profondeurs préférentielles. La majorité des travaux publiés porte sur les Salmonidae, en rivière ou sur de grand plans d'eau comme les Grands Lacs (Nettles et al 1987, Schulz et Berg 1991).

Les émetteurs peuvent être disposés à trois principaux endroits sur le poisson: à la surface (sous la nageoire dorsale), dans l'estomac ou de façon chirurgicale (dans la cavité abdominale) (Mellas et Haynes 1985). Dans les études biotélémétriques, on assume que la fixation d'émetteurs n'influence pas le comportement ou la performance des poissons. Cependant, la position choisie pour l'émetteur dépendra de l'utilisation prévue et de l'espèce en présence. En effet, Mellas et Haynes (1985) ont mené des recherches en laboratoire afin d'évaluer l'incidence d'émetteurs, fixés aux différents endroits décrits plus haut, sur la performance natatoire et le comportement de la Truite arc-en-ciel, *Oncorhynchus mykiss*, et du Bar-perche, *Morone americana*. Il ressort de cette étude que sur l'ensemble des individus utilisés pour l'expérimentation, seule une truite arc-en-ciel avait changé de rang de dominance. De plus, les individus portant l'émetteur de façon externe avaient un temps d'épuisement significativement moins élevé que les autres individus. Peu de cas de maladies

ont été notés chez la Truite arc-en-ciel suivant cette méthode de marquage. Ainsi, si l'on prend en considération tous les facteurs étudiés par ces auteurs, l'étiquetage externe demeure la méthode à préconiser dans le cas de notre expérimentation pour les raisons suivantes: (1) 80% des truites munies d'un émetteur stomacal l'ont régurgité dans les deux premières semaines, (2) la pose d'un émetteur de façon chirurgicale requièrt des manipulations, une anesthésie et des temps de réhabilitation plus importants en plus d'engendrer de plus grands risques d'infections sérieuses, et (3), le temps d'épuisement moins élevé dans le cas d'émetteurs disposés de façon externe a un effet négligeable lorsque l'expérimentation concerne une espèce dont la vitesse de déplacement ainsi que l'endurance ne sont pas des facteurs critiques (Mellas et Haynes 1985).

VARIATIONS INDIVIDUELLES À L'INTÉRIEUR D'UNE MÊME POPULATION

Justification de l'approche basée sur la variation individuelle

La variation individuelle à l'intérieur d'une population peut dépendre de différents facteurs dont l'hérédité, les caractéristiques des individus (physiologiques, morphologiques et comportementales) et les conditions de l'environnement (Ringler 1982, Lomnicki 1988). À long terme, le facteur héréditaire peut permettre de maintenir différentes stratégies à l'intérieur d'une population, signifiant que non seulement la valeur moyenne d'un caractère, mais aussi sa variation, serait adaptative (Maynard Smith 1982). À court terme, la variabilité naturelle dans les caractéristiques des individus et la nature hétérogène de l'environnement peuvent contribuer à la variation du comportement alimentaire ou de la distribution spatiale. C'est pourquoi plusieurs propriétés des populations (i.e. structure d'âge, taux de croissance, fécondité, mortalité) sont directement influencées par les caractéristiques des individus et leurs interactions avec l'environnement (Roese et al. 1991). L'étude de la variation individuelle s'avère donc importante à cause de son effet potentiel sur la dynamique des populations, l'organisation des communautés, la répartition des ressources et la sélection des

proies (Ringler 1982, Lomnicki 1988, Roese et al. 1991, Zebra et Collins 1992).

Conséquemment, les avenues futures en écologie devront tenir compte du fait que les systèmes écologiques sont issus d'individus qui diffèrent entre eux et non seulement suivant leur sexe ou leur âge. Cette idée de différences individuelles n'est pas nouvelle, mais depuis ses débuts, le développement des théories écologiques n'en a pas tenu compte (Lomnicki 1992). En effet, les variations intra- et interindividuelles ont souvent été ignorées ou considérées comme du "bruit" (Ringler 1982). Pourtant, plusieurs évidences montrent que les individus de plusieurs populations diffèrent substantiellement en termes physiologique, morphologique et comportemental. Ringler (1982) en dresse toute une liste dans le cas précis des stratégies d'alimentation chez les poissons d'eau douce. L'existence d'une telle variabilité individuelle reflète l'adaptation des individus à différents micro-environnements (Van Valen 1965) et est une condition nécessaire à l'établissement de pools d'habileté (i.e. au maintient d'une banque de spécialisations individuelles à l'intérieur de la population) (Giraldeau 1985).

L'approche basée sur la variation individuelle n'est pas sans difficulté. Ceci explique en partie pourquoi les écologistes l'ont ignorée si longtemps dans l'étude des populations. Si l'on prend l'exemple des études sur le comportement alimentaire, où l'on cherche à estimer la répartition des ressources à l'intérieur d'une population, on peut facilement l'obtenir en laboratoire pour un individu seul aussi bien que pour un groupe d'animaux ou de plantes pris comme un tout. Par contre, cela devient difficile lorsqu'on cherche à l'évaluer pour un individu en particulier vivant à l'intérieur d'un groupe (Lomnicki 1988). Sachant que la distribution des individus détermine la disponibilité des ressources auxquelles ils ont accès (Roese et al. 1991), l'étude des variations individuelles dans la distribution spatiale semble être une bonne méthode pour estimer la répartition des ressources à l'intérieur de cette population.

Sources de variation

Selon Zerba et Collins (1992), la caractérisation des sources génétiques et écologiques des variations intra-populations est très importante pour évaluer le rôle des individus et leurs implications dans les processus écologiques et évolutionnaires. Ringler (1982) traite séparément les sources de variabilité intra- et interindividuelles, sans que celles-ci ne soient véritablement indépendantes. Il les décrit dans le cas précis des stratégies d'alimentation chez les poissons d'eau douce. Les sources de variation dans le comportement alimentaire entre les individus (interindividuelles) se divisent en trois catégories: les sources physiologiques, morphologiques et comportementales. Dans le premier cas, on retrouve entre autres des variations dans l'acuité des organes sensoriels (vue, odorat, système acoustico-latéralis, système tactile), des différences dans les cycles d'activités de chacun et finalement, le fait que les individus n'ont pas un apétit égal sous des conditions identiques. Les secondes sources de variations interindividuelles sont d'ordre morphologique. Les plus importantes sont les dimensions critiques comme celles du corps, de la mâchoire et des arcs branchiaux (un individu plus grand ou avec une plus grande bouche peut capturer des proies de taille plus importante), la coordination de l'animal qui est le reflet d'une parfaite harmonie entre les nageoires et la forme générale du corps (effet sur la vitesse de nage et la manoeuvrabilité) et évidemment les caractéristiques sexuelles. Enfin, la troisième catégorie regroupe des sources de variation en rapport avec le comportement, comme la vitesse d'apprentissage, le rang de dominance et l'expérience de chacun des individus face à l'environnement et aux différentes proies.

Applications écologiques

La plupart des études récentes portant sur l'individualité appliquent les propriétés des individus aux modèles de stratégies d'alimentation et de dynamique des populations déjà existants, afin de rendre ceux-ci plus réalistes (Lomnicki 1988, Roese et al. 1990, Trebitz 1991, DeAngelis, Godbout et Shuter 1991, DeAngelis et Gross 1992, Breck 1993). Or en

général, ces études se définissent comme étant basées sur les individus, non pas parce qu'elles cherchent à en identifier les différences, mais plutôt parce qu'elles considèrent les individus comme des entités uniques. Par exemple, DeAngelis et al. (1991) utilisent cette approche dans une étude sur la dynamique des populations d'Achigan. Ainsi, plutôt que de considérer uniquement la réponse moyenne de la population, ils conçoivent leurs modèles en faisant varier certaines propriétés des individus comme la taille, l'âge, le taux de croissance, les mouvements, etc.

D'autres études discutent de l'identification et de l'intensité des variations individuelles dans le comportement d'une espèce, en particulier dans le but d'approfondir les connaissances à ce niveau et de poser certaines hypothèses sur les mécanismes qui en sont responsables (Bryan et Larkin 1972, Giraldeau et Lefebvre 1985, Zerba et Collins 1992). À ce sujet, Grant et Noakes (1987) et McLaughlin et al. (1992) ont identifié des variations individuelles dans les tactiques d'alimentation des jeunes de l'année d'Omble de fontaine.

Enfin, certaines études tentent d'évaluer la nature de certaines sources de variation en rapport avec des phénomènes d'individualité décelés chez une espèce en particulier (Ehlinger 1989, Bernstein et al. 1991 et McCarthy et al. 1992). Par exemple, McCarthy et al. (1992) ont démontré l'importance de la hiérarchie sociale sur la variation individuelle dans l'alimentation de la Truite arc-en-ciel, *Oncorhynchus mykiss*.

DESCRIPTION GÉNÉRALE DU PROJET

Ce mémoire de maîtrise comporte trois sections. Dans une première section (CHAPITRE 1), portant sur les variations interindividuelles dans l'utilisation de l'habitat, on traite principalement de l'identification de la variabilité individuelle dans la distribution spatiale entre les individus d'une même population d'Omble de fontaine, et de la relation existant entre ces différences individuelles et certains traits morphologiques et

comportementaux. Cette section est présentée sous la forme d'un article scientifique devant être soumis à la revue "Journal of Fish Biology". La seconde section (CHAPITRE 2) présente l'étude des variations interindividuelles dans l'alimentation de l'Omble de fontaine. On y discute de l'identification de la structure et des déterminants des préférences alimentaires individuelles chez l'Omble de fontaine, en procédant d'une part à une étape descriptive et d'autre part à une approche empirique basée sur la régression multiple. Cette dernière permet d'identifier les facteurs qui influencent (directement ou indirectement) la variation individuelle et de poser des hypothèses plus réalistes concernant les mécanismes responsables de cette variation en nature. Cette section est présentée sous la forme d'un article scientifique soumis à la revue "Canadian Journal of Fisheries and Aquatic Sciences".

Finalement, la troisième section (CHAPITRE 3) présente l'étude des variations intra-individuelles dans l'utilisation de l'espace chez l'Omble de fontaine. On y décrit le patron d'activité locomoteur journalier de l'Omble de fontaine adulte (2+,3+) en lac, lequel est ensuite comparé à celui des jeunes de l'année (0+) et des juvéniles (1+). Cette section est également présentée sous la forme d'un article scientifique qui sera soumis à la revue "Journal of Fish Biology".

CHAPITRE 1

Individual variations in habitat use and morphology in brook charr, *Salvelinus fontinalis*.

Abstract. The specific objectives of this study were to determine if there is individual specialization in habitat use by lacustrine brook charr, *Salvelinus fontinalis*, and if so, if specialization is related to fish morphology, thermal preferences, and spawning site selection. Localizations and ambient temperatures of 28 brook charr equipped with thermosensitive radio-transmitters were recorded during three summers (1991, 1992, and 1993) in two lakes of the Mastigouche Reserve (Québec, Canada). Fifty percent of the fish were found mainly in the benthic zone (hereafter benthic individuals), 18% in the pelagic zone (pelagic individuals), and 32% travelled regularly between the two zones (generalist individuals). The observed inter-individual differences in habitat preference were related to differences in morphology, coloration and variability in ambient temperature: (i) the pectoral fins of benthic and generalist individuals were significantly longer than those of pelagic ones; (ii) the coloration of the lower flank of benthic and generalist individuals was silver-grey while that of pelagic individuals was red; (iii) although the between-individual variance of the daily ambient temperature tended to differ among the three groups, no significant difference was found in their mean ambient temperature; (iv) the coefficient of variation of the mean ambient temperature was significantly higher for the benthic individuals than for the generalist ones. At the beginning of the 1992 spawning season, nine transmitters were still working; four of the nine tracked individuals moved among three inlets identified as spawning grounds before finally selecting one. At the end of this spawning season, the four pelagic individuals were found in one inlet, the only benthic individual in another inlet, while three generalists were distributed among the three inlets, supporting the hypothesis that benthic and pelagic individuals may select different spawning grounds. One generalist individual did not move to the spawning grounds.

INTRODUCTION

Individual variability in foraging and habitat use by animals of the same cohort has long been ignored because it was considered as "ecological noise" around a mean or an optimal response (Ringler, 1983; Lomnicki, 1988). Although individual variability in feeding habits was well described by Ivlev (1961) and Bryan & Larkin (1972), its ecological significance in terms of resource partitioning, optimal foraging, population dynamics and community structure is just recently being recognized (Curio, 1976; Chesson, 1978; Morse, 1980; Dill, 1983; Ringler, 1983, 1985; Ehlinger, 1990). For example, resource partitioning among individuals may allow habitats to support more dense populations than they would otherwise and facilitate survival under marginal conditions (Morse, 1980). There is also increasing theoretical evidence that individual variability may have significant consequences for population dynamics and community structure (e.g. Lomnicki, 1988; DeAngelis & Gross, 1992; Winkle & Rose, 1993; Tyler & Rose, 1994). On a long-term basis, hereditary factors could maintain different strategies within populations, so that not only the mean value of a trait but also its variation may be adaptive (Maynard Smith, 1982; Lomnicki, 1988).

There are essentially two short-term components of individual variability: the *within-individual* component, which represents the average resource diversity used by a single individual, and the *between-individual* component, which represents the resource diversity used by different individuals in a population (Roughgarden, 1972, 1979). In a review of variation in foraging tactics of fishes, Ringler (1983) pointed out that between individual variability may derive from physiological, behavioural and morphological sources such as visual acuity, hunger state, experience, learning, social interactions, and critical morphological dimensions, while within-individual variability may be caused by specific physiological states (hunger, acclimation) and behaviourial contexts (experience, prey type or distribution, motivation).

In fish, most of the available information on between-individual variability comes from laboratory and mark-recapture experiments (e.g. Bryan & Larkin, 1972; Ehlinger, 1990) and from dead individuals obtained by fishing (e.g. Ivlev, 1961; Venne & Magnan, 1995), while information concerning within-individual variability has been obtained only from laboratory experiments (e.g. Ringler, 1985; Ehlinger, 1989, 1990; McCarthy *et al.*, 1992). It is important to assess the two components of individual variability on free-living fish to estimate their real occurrence in the field, support hypotheses concerning underlying mechanisms and adaptive significance, and document assumptions of individual-based models.

The objective of the present study was thus to investigate the individual variation in habitat use by brook charr, *Salvelinus fontinalis* (Mitchill), in two lakes, using radio-telemetry. As many population-level properties (i.e. age structure, birth and death rate) can be directly influenced by the spatial location of individuals, e.g. through differential resource availability, their habitat use is a key component of population dynamics (Roese *et al.*, 1991). The brook charr is a generalist carnivorous species (Scott & Crossman, 1974; Power, 1980; Magnan, 1988; Lacasse & Magnan, 1992) which has colonised lakes of the Canadian Shield after the last glaciation. Its morphology allows individuals to feed on the two main functional prey types found in these lakes (i.e. zoobenthos in the littoral zone and zooplankton in the pelagic zone; Tremblay & Magnan, 1991) and thus the brook charr represents a good model species for studying individual specialization. The specific objectives of the study were to determine if there is individual specialization in habitat use by brook charr in these lakes and if so, if it is related to fish morphology, thermal preferences, and spawning site selection.

MATERIALS AND METHODS

STUDY LAKES

The study was carried out in Lake de L'Épervier (1991) and in Lake Ledoux (1992, 1993), located in the Mastigouche Reserve (46°38'N, 73°15'W), Québec (Canada). These lakes are typical of small oligotrophic temperate zone lakes with respect to surface area (8.4 and 11.9 ha), mean depth (5.6 and 5.5 m), conductivity (18.1 and 21.3 $\mu S\ cm^{-1}$), dissolved oxygen, thermal stratification, and Secchi disk transparency (Magnan, 1988; Lacasse & Magnan, 1992). Brook charr and northern redbelly dace, *Phoxinus eos* (Cope), are the only fish species in the lakes. The two lakes are 10 km apart, are subject to sportfishing, and exploitation is carefully controlled by the Québec Government (Magnan, 1988). The lakes were closed to sportfishing during the study.

MARKING

In June or July of each summer (Table I), 20 adult brook charr (250-419 mm fork length) were tagged with 4g thermosensitive radio-transmitters (model 357, Advanced Telemetry Systems, ATS, Minnesota, USA). Fish were captured with experimental multifilament gillnets (1.8 m deep by 38.1 m long, with stretched mesh sizes of 2.5, 3.8, 6.4, and 7.6 cm) arbitrarily set perpendicularly to the shore, mainly in the littoral zone. Gillnets were removed every 15 minutes and only fish in good condition, usually those caught by the teeth, were retained for marking.

Transmitters were attached externally under the dorsal fin after the fish were lightly anaesthetized with tricaine methanesulphonate (MS-222). Fixation was made with nylon monofilament threaded through muscular tissues at two points. The transmitter was placed on one side of the fish while on the other side the filament and fixation knot were kept apart from the fish by a small rubber plate (Winter, 1983). A neoprene cushion was placed between the fish and the rubber plate to avoid lesions due to rubbing on teguments. In 1992

Table I. Mean fork length of brook charr used in the study and sampling periods for fish localizations.

Lake	Year	n	Mean fork length (mm)	S.D. (mm)	Range (mm)	Sampling period	Number of days
Épervier	1991	4	341	18	325-360	29 June to 29 August	59
Ledoux	1992	11	343	45	250-400	21 July to 30 October	87
Ledoux	1993	13	389	30	320-419	22 July to 28 October	93

and 1993 (Lake Ledoux), the fish were measured and photographed over a ruler before release. In 1991 (Lake de l'Épervier) the fish were kept for 2h in a holding enclosure (littoral zone) before releasing them into the lake. A total of four fish survived these manipulations in 1991 (Lake de l'Épervier) compared to 11 in 1992 and 13 in 1993 (Lake Ledoux). In 1991, longer manipulations and holding periods in the enclosure were probably more stressful for the fish and were thus responsible for the higher observed mortality. In 1992 and 1993, manipulation time was much reduced by using a cone-shaped needle rendering thread insertion easier, and by eliminating the post-operatory holding period. Also, colder water than in 1991 was used in the manipulation basin. The tagging process usually lasted less than one minute per fish. In each of the three years, most of the mortality occurred during the 10 days following marking. All of the fish that were alive after 10 days were tracked until the transmitter batteries were exhausted. Mean fork length of fish and periods of tracking are shown in Table I. The length (mm) of the mouth (anterior end to posterior end of maxilla) and the pectoral fin, height of the caudal peduncle, and eye diameter were obtained from photographs of the left side of the fish taken in 1992 and 1993.

To quantitatively evaluate the apparent link between spatial preferences of individuals and their coloration pattern, five persons were asked to classify individuals into two distinct groups based on the coloration of their lower flank on photographs; a "red" group and a "non-red" group. We then compute a percent of correct classification based on the evaluation of the five persons. This classification was then compared to the one obtained from the spatial preferences of individual fish.

FISH LOCALIZATION

Localization of individual brook charr was done on average every two days during each sampling period (Table I) using a radio receiver (model R2000, ATS, Minnesota, USA) equipped with a loop antenna. On each sampling date, the horizontal (x and y)

coordinates of each fish were determined during the daylight period (8:00 to 18:00) by triangulation, using a compass and landmarks spaced regularly around the lakes. Fish depth (z coordinate) was determined by comparing the temperature of the fish surroundings, measured by the thermosensitive transmitter (hereafter ambient temperature), and the thermal profile of the lake measured on the same sampling date. This procedure was sensitive enough to determine if a fish was in the epi-, meta- or hypolimnion. For each sampling date, the ambient temperature was recorded on four different occasions: when each fish was localized (to determine their vertical position according to the thermal profile of the lake), and at the beginning, middle, and end of the period in which all individuals were localized, which lasted approximately 2h in 1991 and 4h to 6h in 1992 and 1993. The ambient temperature of a given fish was calculated as the mean of the four measurements. For each fish localization the lake depth was measured also with a graduated cord to position the individuals more accurately on the bathymetric map. On eight occasions between 1991 and 1993, a total of five to seven individuals were localized every 4h during complete 24h cycles.

PRE-SPAWNING MOVEMENT

In 1992, the fish were tracked until they migrated to their spawning sites in three different inlets. The relationship between the spatial preferences of individuals during summer and the selection of a spawning site was evaluated. In 1993, the fish were not yet on the spawning grounds on October 28. After this period the lake could not be reached due to snow accumulation.

STATISTICAL ANALYSES

The zone where each fish was located was coded using the following method: the lake volume was first divided according to thermal stratification (epilimnion, metalimnion, and hypolimnion) and then, each stratum was divided into zones associated with the bottom

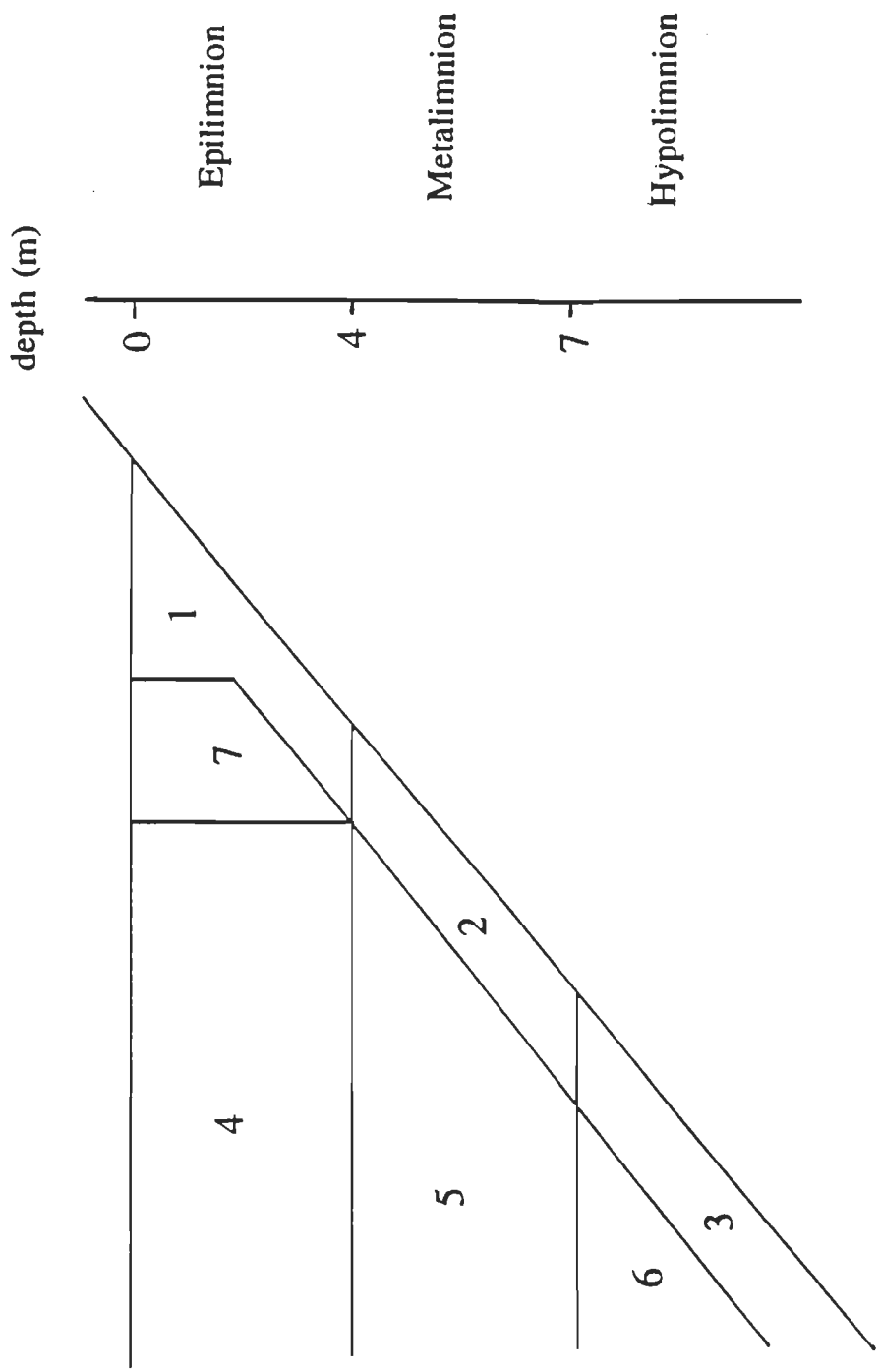
(up to 1m from the bottom; zones 1 and 2; Fig. 1) and zones associated with the open water (zones 4, 5 and 6; Fig. 1). Zones 1 and 2 will be referred to hereafter as the "benthic zone" and zones 4, 5 and 6 as the "pelagic zone" (Fig. 1). Localizations in zones 3 and 7 (Fig. 1) were not considered in the analyses because they were difficult to assign to one of the above ecological zones. No fish were localized in zone 7 and only 1% of the 486 localizations were done in zone 3. For each sampling date, fish depth, lake depth, ambient temperature, and thermal profile of the lake were used to ascribe fish to one of these zones.

The between- and within-individual ambient temperature variances, computed by analysis of variance (ANOVA), were compared to evaluate the inter-individual differences and the intra-individual variations in the thermal preferences. In this analysis, the mean daily temperature of each individual fish was used as the sampling unit. This analysis was performed only for fish tracked in lake Ledoux (1992-1993) to prevent possible bias due to inter-lake variation in thermal regimes, and only for localizations made before the late summer loss of thermal stratification.

Only the fish localizations done during the thermal stratification of the lakes were considered in the analysis of spatial distribution and thermal preferences.

Pearson correlation coefficients were computed between each morphological trait (adjusted for fish size; Packard & Broadman, 1988) and the frequency of occurrence (%) of fish in benthic zone (zone 1 and 2; Fig. 1), to evaluate the relationship between morphological characteristics and habitat use.

Figure 1



RESULTS

SPATIAL DISTRIBUTION

Individual brook charr were arbitrarily classified as "benthic" or "pelagic" individuals, when they were localized over 60% of the time in one of the two zones, and as "generalist" individuals when they travelled regularly between the two zones. Of the 28 individuals tracked during this study, 14 were classified as benthic, five as pelagic, and nine as generalist. Benthic individuals were localized in the benthic zone 81.7 ± 9.7 % of the time (mean ± S.D.), while pelagic individuals were localized in the pelagic zone 68.6 ± 4.7 % of the time. Generalist individuals were found in the benthic zone 48.7 ± 6.4 % of the time (approximately the same time as in the pelagic zone; Fig. 2).

Individuals were much more active during the night (22:00-6:00) than during the day (10:00-18:00) according to the distance travelled between two consecutive localizations (night: 26.2 ± 18.7 m/h; day: 12.4 ± 15.8 m/h; n = 64). However, no significant difference was found in the mean distance travelled between two consecutive localizations among benthic, pelagic, and generalist individuals (night: $F = 0.02$; $p > 0.05$; day: $F= 0.96$; $p > 0.05$).

Based on the frequency of occurrence of fish in each zone, benthic individuals were more faithful to the benthic zone than were pelagic ones to the pelagic zone (81.7 ± 9.7 % versus 68.6 ± 4.7%; $F = 81.9$, $p < 0.0001$).

AMBIENT TEMPERATURE

The ANOVA showed that the within-individual variance of the ambient daily temperature was much lower than the between-individual variance, whether the data of all 24 fish used in this analysis or the three groups defined in the above section were examined (Table II). Although the between-individual variance of the daily ambient temperature tended to differ among the three groups (Table II), no significant difference was found in

Figure 2

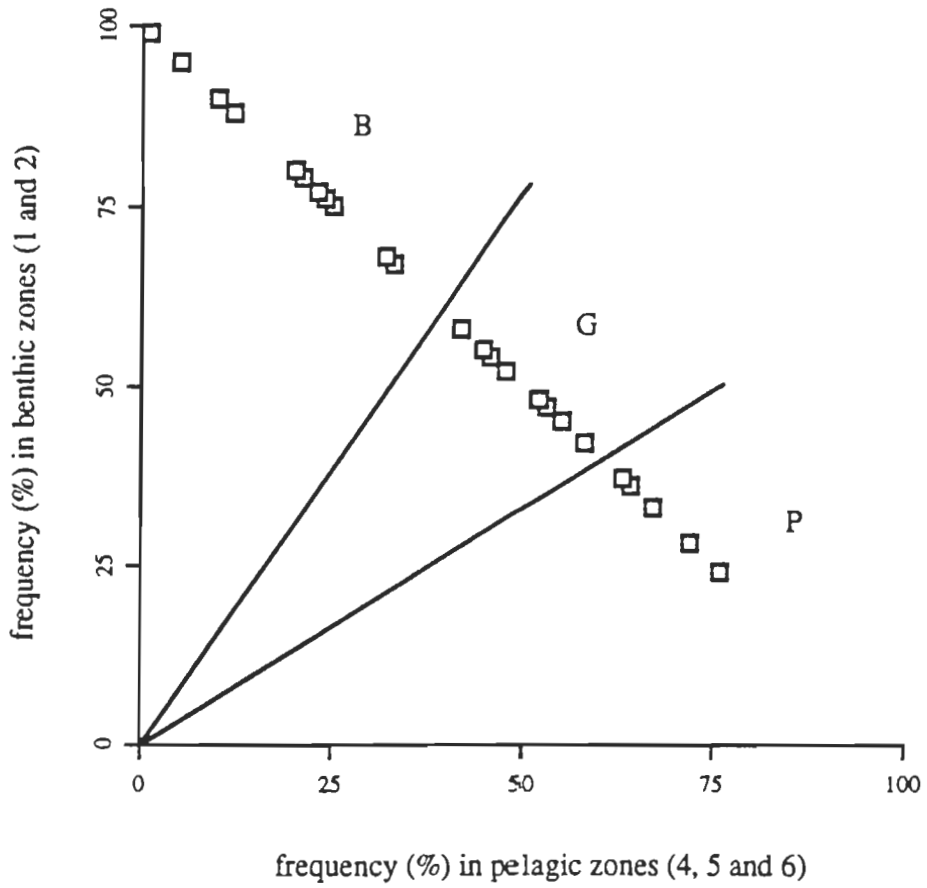

frequency (%) in benthic zones (1 and 2)
100
75
50
25
0
B
G
P
0
25
50
75
100
frequency (%) in pelagic zones (4, 5 and 6)

Table II. Within- and among-individual variation in the ambient temperatures at which brook charr were localized during the study (1992-1993); all individuals, benthic, pelagic, generalist individuals.

Source of variation	Sum of squares	d.f.	mean squares	MS among / MS within
		All individuals		
total	4095.3	609		
among individuals	2146.1	23	93.3	28.1
within individuals	1949.1	586	3.3	
		Benthic individuals		
total	2711.7	309		
among individuals	1593.9	12	132.8	35.3
within individuals	1117.8	297	3.8	
		Pelagic individuals		
total	563.0	117		
among individuals	204.0	3	68.0	21.6
within individuals	359.1	114	3.1	
		Generalist individuals		
total	655.9	181		
among individuals	183.5	6	30.6	11.3
within individuals	472.4	175	2.7	

their mean ambient temperature ($F = 0.98$; $p>0.05$; Table III). The coefficient of variation of the mean ambient temperature was however significantly higher for the benthic individuals than for the generalist ones ($F = 6.8$; $p<0.05$; Table III), indicating that inter-individual ambient temperature is more variable in the benthic group than in the generalist group.

MORPHOLOGICAL CHARACTERISTICS AND COLORATION PATTERN

The length of the pectoral fin was positively correlated with the occurrence of individuals in the benthic zone (Table IV). The adjusted mean length of the pectoral fin of benthic (5.2 ± 0.5 mm) and generalist (4.9 ± 0.4 mm) individuals was significantly higher than that of pelagic ones (4.1 ± 0.5 mm; ANCOVA, $F = 6.63$, $p < 0.007$). No other morphological characteristics were significantly correlated with the occurrence of brook charr in the benthic zone, including the length of the mouth, which however tended to be related to the occurrence of fish in the benthic zone, (Table IV).

Based on the classification of individuals according to their colour pattern, all of the four pelagic fish were classified as "red" while all of the 13 benthic fish and six of the seven generalist fish were classified as "non-red", for an overall 96% of good reclassification.

PRE-SPAWNING MOVEMENT

At the end of October 1992, all fish had selected a spawning site (Fig. 3). All the pelagic individuals selected inlet #2, the single benthic individual tracked at this time selected inlet #1, while generalist individuals were found in the three inlets (Fig. 3). Fish number 430, a generalist, did not move to these spawning sites (Fig. 3).

In the weeks preceding the spawning ground selection, four of the nine fish moved among two or the three inlets before selecting one (Fig. 4). For example, fish number 410 began the pre-spawning period by visiting inlet #1. Two weeks later, it moved to inlet #3 before selecting inlet #2 at the end of autumn (Fig. 4).

Table III. Mean ambient temperature with standard deviation (S.D.) and coefficient of variation for the benthic, pelagic, and generalist brook charr from Lake Ledoux 1992,1993.

Group	n	Mean[1]	S.D.	C.V.[2]
Benthic	13	11.9	2.3	19.4_a
Pelagic	4	13.0	1.5	11.7_{ab}
Generalist	7	12.9	1.1	8.7_b

[1] No significant difference in mean temperature among groups as determined by an ANOVA

[2] Coefficients of variation with the same letter are not significantly different as determined by a Lewontin comparison test (Zar, 1984).

Table IV. Pearson correlations between morphological characteristics and the occurrence of individuals in the benthic zone.

Variable	n[1]	r	p
Fish length	28	-0.08	0.718
Length of pectoral fin	21	0.64	0.002
Length of mouth	24	0.42	0.056
Height of caudal peduncule	18	0.25	0.390
Eye diameter	22	0.20	0.340

1: It was not possible to measure all the characteristics on each fish due to the presence of artifacts on some of the pictures, such as reflection of light on the water surface.

Figure 3

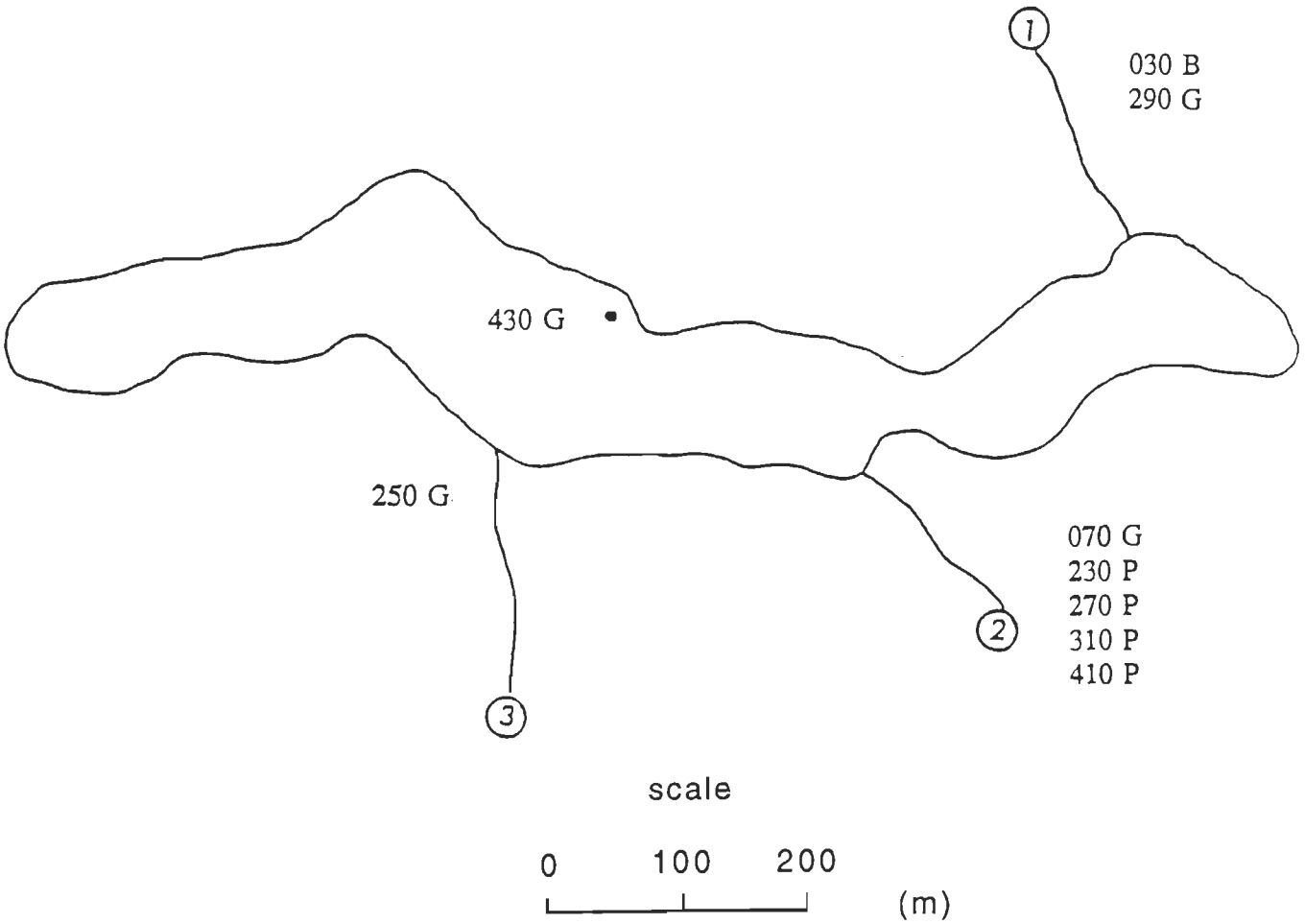
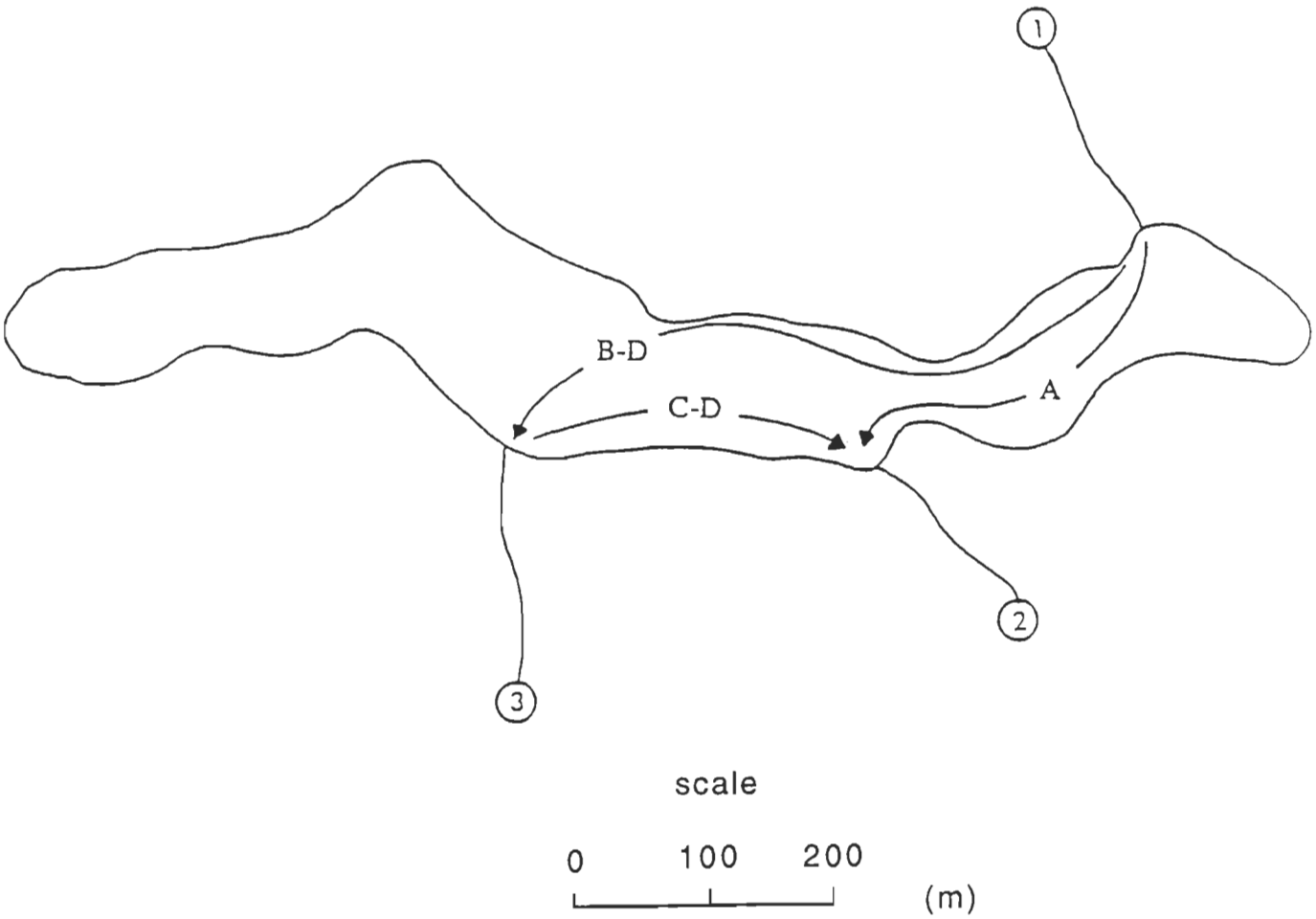

1
030 B
290 G
430 G
250 G
070 G
230 P
270 P
310 P
410 P
2
3
scale
0
100
200
(m)

Figure 4



DISCUSSION

The results of this study show inter-individual differences in habitat use by brook charr. Fifty percent of the fish were found mainly in the benthic zone, 18% in the pelagic zone, and 32% travelled regularly between the two zones. The ecological significance of the three groups identified is reliable because each individual showed a given preference over a minimum of two months of tracking. Furthermore, the study was done in two lakes, over three different summers. These inter-individual differences in habitat use suggest inter-individual differences in resource utilization. Two studies based on gill net fishing in lakes of the same area support this hypothesis; the diet of 1+, 2+, and 3+ brook charr is related to their spatial distribution between the littoral and pelagic zones (Tremblay & Magnan, 1991), while the diet of 0+ brook charr is related to the distribution of individuals between the littoral and profundal zones (Venne & Magnan, 1995).

The higher proportion of benthic individuals in the present study may be related to ecological factors such as the profitability of littoral habitat. There is evidence that brook charr feed preferentially on benthic organisms of the littoral zone in this system; in allopatry, individuals feed mainly on zoobenthos, while in sympatry with white sucker, *Catostomus commersoni* (Lacépède), they shift to feeding on zooplankton in the pelagic zone (Magnan, 1988; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992). As white sucker is absent from lakes Ledoux and de l'Epervier, it is possible that a high proportion of brook charr selected the benthic habitat. Recent *in situ* experiments also suggested that the littoral zone is more profitable than the pelagic zone for brook charr, in terms of the net energy intake (Joules day^{-1}) in each habitat (Héroux & Magnan, unpublished data). Alternatively, the higher proportion of benthic individuals may be due to sampling bias; as the gill nets were mainly effective in the littoral zone (see Materials and Methods section) it is possible that more benthic individuals were sampled and then tracked.

The observed inter-individual differences in habitat preference were related to differences in morphology, coloration, and variability in ambient temperature. The pectoral fin of benthic and generalist individuals was significantly longer than that of pelagic ones. Long pectoral fins are related to the slow and precise manoeuvring (Gatz, 1979; Webb, 1984) required to feed on benthic organisms on the bottom, while shorter pectoral fins are associated with cruising, which is necessary for searching efficiently in the open water habitat (Ehlinger, 1990). A similar relationship between length of pectoral fin and foraging behaviour was found for bluegill sunfish, *Lepomis macrochirus* (Rafinesque), (Ehlinger, 1990), suggesting a strong functional relationship between pectoral fin morphology and feeding tactics in fishes. Also, as for bluegill sunfish, other differences in morphology related to habitat selection were observed in young-of-the-year brook charr (Venne & Magnan, 1995), suggesting that such functional relationships can occur early in the life history of fishes (Ehlinger, 1990).

The lower flank coloration of benthic and generalist individuals was silver-grey while that of pelagic individuals was red. In fish, red coloration is mainly due to carotenoid pigments (Brush & Reisman, 1965; Fujii, 1993). Carotenoids cannot be synthetised by the fish and must be acquired through the diet (Fujii, 1993). If the spatial distribution of pelagic individuals is effectively correlated with a rich zooplankton diet, their red coloration suggests that there is a high carotenoid content in these pelagic prey. It is known that copepods are a major source of carotenoids (Folstad *et al.*, 1992) but they were rarely found in stomachs of brook charr (Magnan, 1988; Lacasse & Magnan, 1992), suggesting that the red coloration is due to carotenoid contained in other zooplankton found in their diet, such as cladocerans. It is noteworthy that generalist individuals are similar to benthic ones as regards the length of the pectoral fin and coloration pattern, two traits apparently related to diet. There is evidence that these differences were not related to sexual dimorphism, which is characterized by differences in the general shape of the body (male body are more laterally compressed and deeper, and have a small kype or hook on the lower jaw) and in

fin, jaw and dorsal coloration (Power, 1980). Also, later sampling done as a follow up of this project revealed that 25% of the silver grey individuals were male and that 29% of the red ones were female (P. East & P. Magnan, personal observations).

The absence of significant differences in mean ambient temperature among benthic, pelagic, and generalist individuals as well as the very low within-individual variance in this parameter highlights the importance of temperature in the bioenergetics of these fish. The final preferendum and optimal growth temperature of brook charr average 15.4°C in a review by Wismer & Christie (1987). As temperatures selected by fish in the field are generally lower than laboratory estimates (by ~1°C; Magnuson *et al.*, 1979; Christie & Regier, 1988), the selected temperature of individuals in this study (12.4 ± 2.6°C) is quite close to the optimal values. Also, following Christie & Regier (1988) the *optimal thermal niche* of brook charr ranges between 12.4 and 16.4°C (± 2°C around the final preferendum, skewed 1°C lower). Thus, the present results suggest that "cold water" species such as brook charr will effectively select the colder temperatures in this range. On the other hand, the significantly higher variability in mean ambient temperature of benthic individuals may reflect thermoregulatory diel migrations between the feeding area (littoral zone), which is usually above 20°C during the summer months, and a thermal refuge area deeper in the water column. In Lake Ledoux, almost all benthic individuals were localized in the area where the slope of the lake was steepest (~ 45°). Because of vertical thermal stratification, this could allow individuals to minimize the horizontal movement between feeding and thermal refuge areas, thus supporting the above hypothesis. Such behavioural thermoregulation was observed in another salmonid fish, sockeye salmon, *Oncorhynchus nerka* (Walbaum), in a similar system (Brett, 1971). Venne & Magnan (1995) also observed that the length, weight, and condition factor of young-of-the-year brook charr were more variable for a littoral than for a profundal group, suggesting more variable environmental conditions in the littoral zone.

The results of the present study support the hypothesis that ecotypes of the same species (here benthic and pelagic individuals) may select different spawning grounds. At the beginning of the 1992 spawning season, four of the nine tracked individuals moved among the three identified spawning grounds before finally selecting one. At the end of this spawning season, the four pelagic individuals were found in one inlet, the only benthic individual in another inlet, while three generalists were distributed in the three inlets. The results of O'Connor & Power (1973) support the hypothesis of homing in brook charr in one lake containing two spawning grounds. Because of the small sample size of reproductive individuals in the present study, further work will be needed to evaluated this hypothesis.

Correlations between morphology and specific behaviour of individuals (this study, Grant & Noakes, 1987; Ehlinger & Wilson, 1988; Ehlinger, 1990) address the question of within-individual stability of these behaviours in the field. The present results show that habitat use by brook charr did not reflect frequent and random changes in fish distribution but corresponded instead to relatively stable habitat use in most individuals (i.e. benthic and pelagic). The results also indicated that approximately a third of marked individuals were generalists showing no specific preference for a given habitat. In a mark-release experiment, Bryan & Larkin (1972) studied food specialization of brook charr, cutthroat trout, *Salmo clarki* (now *Oncorhynchus clarki*), and rainbow trout, *Oncorhynchus mykiss*, in a stream and ponds. Their results showed that the degree of individual specialization was high over short periods of time and that some specialization persisted for over half a year. No striking correlations were found between degree of specialization and individual characteristics such as size, growth rate, or weight and number of food items, previous specialization, and area of capture (Bryan & Larkin, 1972). In a study of foraging movements of recently-emerged brook charr in still-water pools, McLaughlin *et al.* (1994) found no correlation between foraging behaviour (sedentary versus active fish) and body size or shape of individuals. Although most fish tended to specialize at one role, some individuals clearly switched

between the two modes while they were foraging, over the duration of the observations. In another study, McLaughlin & Grant (1994) found significant differences in morphology of recently emerged brook charr foraging in slow versus fast running water, two more contrasting environments. The results reported above and those of the present study suggest that differences in morphology, as well as stability of within-individual behaviours, will occur only when available habitats require specific abilities (e.g. fast versus slow swimming in streams; slow and precise manoeuvring versus cruising in littoral and pelagic zones of a lake). The magnitude of these differences should also be related to the degree of difference among habitats.

Whether such inter-individual differences in morphology and behaviour are of phenotypic or genotypic nature is still unknown. Morphological differences appear very early in the life history of brook charr (McLaughlin & Grant, 1994; Venne & Magnan, 1995) and bluegill sunfish (Layser & Clady, 1987), and the potential for reproductive isolation (as suggested in this study) could maintain underlying genetic variation among individuals. On the other hand, inter-individual differences may result from phenotypic variation among individuals (e.g. experience, learning; Ringler, 1983) or by environmental characteristics acting on a single "plastic" genotype (see Ehlinger, 1990). In this context, morphological differences among individuals may result from different foraging tactics *per se* (like a "training effect").

Whether they are genotypic or phenotypic, the inter-individual variations may have quite important effects on population dynamics and related theory. As occurs at the interspecific level, such resource partitioning could allow a population to reach higher densities and also promote survival under marginal conditions in one microhabitat (Morse, 1980). Furthermore, persistent differences among individuals oppose the traditional concept of "single best solution" predicted by optimal foraging theory (Krebs & McCleery, 1984; Stephens & Krebs, 1986). As suggested by Ehlinger (1990), such variation among individuals does not necessarily indicate that some individuals are "suboptimal" but may

actually reflect the balance between the costs and benefits of within-individual behavioural flexibility relative to between-individual stereotypy. In this context, recent modifications of the ideal-free distribution model of density-dependent habitat selection (Fretwell & Lucas, 1970) take into account phenotypic differences in foraging ability and predict different optimal strategies for individuals in a population (Parker & Sutherland, 1986).

The investigation of proximate mechanisms underlying individual variability in trophic morphology and behaviour and the testing of models considering such phenotypic differences among individuals will certainly be featured among the next challenging research problems in animal ecology.

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Figure captions

Fig. 1. Classification of the different zones for statistical analyses; 1 and 2: benthic zones; 4,5 and 6: pelagic zones; 3 and 7: intermediate zones; not included in statistical analyses.

Fig. 2. Frequency of occurrence of the 28 brook charr in benthic (1 and 2) and pelagic zones (4, 5 and 6). B, G, and P represent "benthic", "generalist", and "pelagic" individuals respectively.

Fig. 3. Localization of individual brook charr in the spawning sites at the end of the sampling period (Lake Ledoux 1992). Inlets are represented by circled numbers. Each number represents an individual fish. B, G, and P represent "benthic", "generalist", and "pelagic" individuals respectively.

Fig. 4. Selection of spawning sites (Lake Ledoux 1992). Inlets are represented by circled numbers. Each letter represents an individual fish.

CHAPITRE 2

Structure and determinants of interindividual variations in the diet of brook charr, *Salvelinus fontinalis*.

Abstract. We investigated the structure and determinants of interindividual variations in the diet of brook charr, *Salvelinus fontinalis*, from a data base containing biotic and abiotic descriptors of 70 lakes of the Canadian Shield (Québec, Canada) and data on the stomach contents of 3776 charr. In any given lake, some of the charr fed almost exclusively on benthic organisms ("benthic specialists", i.e., mean percent weight of benthic prey > 90%), others, almost exclusively on pelagic prey ("pelagic specialists", i.e., mean percent weight of benthic prey < 10%), and the rest were "generalist feeders" (i.e. mean percent weight of benthic prey between 10% and 90%). The proportion of benthic specialists was related to the intensity of competition for benthic organisms with creek chub, *Semotilus atromaculatus*, and white sucker, *Catostomus commersoni*. The effect of white sucker was more pronounced than that of creek chub: the proportion of benthic specialists among brook charr decreased from 41.3% in allopatry to 19.7% in sympatry with creek chub, and to 9.9% in sympatry with white sucker. Other independent variables related to zoobenthos abundance (lake depth, lake area, season) were also determinants of diet specialization in brook charr. Finally, we found maked differences among the diets of benthic specialists, with individual fish consuming only a part of the entire spectrum of taxa available in the benthic habitat.

Introduction

Although individual variation in diet composition of fish was well described by Ivlev (1961) and Bryan and Larkin (1972), its ecological significance has long been ignored because individual variation was considered as "noise" around a mean response (Ringler 1983; Lomnicki 1988). It is only recently that the potential role of individual variability in prey selection, resource partitioning, population dynamics, community structure, and optimal foraging has received widespread recognition (Curio 1976; Chesson 1978; Morse 1980; Dill 1983; Ringler 1983; 1985; Lomnicki 1988; Ehlinger 1990; DeAngelis and Gross 1992; Winkle and Rose 1993; Tyler and Rose 1994).

There are essentially two short-term components of individual variability: the *within (or intra) individual* component, which represents the average resource diversity used by a single individual, and the *between (or inter) individual* component, which represents the resource diversity used by different individuals in a population (Roughgarden 1972; 1979). In a review of variation in foraging tactics of fishes, Ringler (1983) pointed out that *inter-individual* variability may derive from physiological, behavioural, and morphological sources such as acuity, hunger state, experience, learning, social interactions and critical morphological dimensions, whereas *intra-individual* variability may be caused by specific physiological states (hunger, acclimation) and behavioural contexts (experience, prey type or distribution, motivation).

The brook charr, *Salvelinus fontinalis,* is a generalist carnivorous species (Scott and Crossman 1977; Power 1980; Magnan 1988; Lacasse and Magnan 1992) which colonised lakes of the Canadian Shield after the last glaciation. Brook charr feed on the two main functional prey types found in these lakes, zoobenthos in the littoral zone and zooplankton in the pelagic zone, in varying proportions (Tremblay and Magnan 1991), and thus this species represents a good model for studying individual variations in diet. The intra- and interindividual variations in the use of littoral and benthic habitats by brook charr were investigated with radio-telemetry in another study (Bourke *et al.*, submitted). The main goal

of the present study was to investigate interindividual variation in the diet of brook charr, using a database containing information on biotic and abiotic characteristics of 70 lakes situated on the Canadian Shield. The specific objectives of the study were to (1) describe the structure of interindividual variations in the diet of brook charr in different fish communities, (2) evaluate the determinants of interindividual variation in diet, and (3) evaluate the degree of dietary variation of individuals within a given habitat.

Materials and methods

Data base

The present study is based on stomach content analyses of 3776 brook charr captured in 70 lakes located in the Mastigouche (46°40'N, 73°20'W) and St-Maurice (45°05'N, 73°15'W) Reserves, Québec, Canada. Data on diets as well as on other biotic (fish community composition, fish size, sex, and age) and abiotic (date and hour of capture, lake morphometry, physicochemistry, thermal habitat, littoral habitat structure) features of the study lakes were obtained from seven studies done previously in this system (Magnan 1988; Lachance and Magnan 1990; Tremblay and Magnan 1991; East and Magnan 1991; Lacasse and Magnan 1992; Venne and Magnan 1995; Lapointe and Magnan, unpublished data. Each of these study was considered as one data set. These studies mainly evaluated the impact of white sucker, *Catostomus commersoni*, and creek chub, *Semotilus atromaculatus*, on the diet of brook charr populations. The relative contribution of the spatial structure and environmental variables on the diet of charr also has been evaluated in this system (Lacasse and Magnan 1992; Magnan *et al.* 1994). These earlier studies analysed the "mean response" of the populations based on the mean percent weight of different prey categories (Hyslop 1980). In the present study, we address instead questions about interindividual dietary variation.

Study Lakes

The study lakes ranged from 3.9 to 500.8 ha in surface area, and from 2.5 to 17.6 m in mean depth. Of the 70 study lakes, 29 contained allopatric brook charr populations, 24 contained brook charr and creek chub, and 16 contained brook charr and white sucker. We hereafter refer to these as "brook charr lakes", "brook charr and creek chub lakes", and "brook charr and white sucker lakes", respectively. Northern redbelly dace, *Phoxinus eos*, was present in almost all lakes but its presence did not significantly affect the mean yield of brook charr in the exploited lakes of the Saint-Maurice and Mastigouche Reserves (P. Magnan, unpublished data). Creek chub and pearl dace, *Semotilus margarita*, were also present in some of the brook charr and white sucker lakes, but gillnet fishing in three of these lakes indicated that their relative biomass represented less than 1% of the total fish biomass (P. Magnan, unpublished data). All lakes were subject to sportfishing, and exploitation was carefully controlled by the Québec government.

Samples

A mean of 20 stomachs per lake and date was collected from brook charr captured by angling (sport fishers) or by gillnet fishing, depending on the study. Stomach samples for each lake and date were grouped by fish size class (>200 mm total length, TL and <200 mm TL). Sport fishers were given a cooler in which they could retain captured brook charr without eviscerating them. Upon the angler's return, or immediately after capture (gillnet fishing), the total length of each brook charr was recorded and its stomach was removed and preserved in a 10% formaldehyde solution. In the laboratory, the weight of different prey categories was estimated as dry weight (± 0.01 mg) of prey identified to order or family in Tremblay and Magnan (1991), Lachance and Magnan (1990), Venne and Magnan (1995), and Lapointe and Magnan (unpublished); and wet weight (± 0.01 mg) of the following prey categories in Magnan (1988), East and Magnan (1991), and Lacasse and Magnan (1992): zoobenthos, amphipods, zooplankton, dipteran pupae, swimming insects,

terrestrial insects, and prey-fish.

Independent Variables

Independent variables that could vary over a short period (e.g. chemical variables) were measured within 1-4 day following stomach sampling, between 10 and 17 h. Two dummy variables coding for creek chub and white sucker presence were created to describe the fish species composition of the study lakes; two zero values were given to brook charr lakes, 1 and 0 to brook charr and creek chub lakes, and 0 and 1 to brook charr and white sucker lakes (Lacasse and Magnan 1992). Fish species distributions were obtained from the Ministère de l'Environnement et de la Faune du Québec (MEF). Lake area (m^2), littoral area (0-2 m depth; m^2), lake volume (m^3), shoreline length (m), maximum depth (m), and island area (m^2) were calculated from bathymetric maps available from the MEF or Lacasse and Magnan (1992). Water temperature (°C), dissolved oxygen (mg/l), pH, and conductivity (µS/cm) were measured at 0.5 m from the surface at the deepest point of each lake with a Hydrolab Surveyor II (model SVR2); water transparency was measured with a 20-cm Secchi disk and an underwater viewer (Lacasse and Magnan 1992).

The following habitat characteristics were obtained from Lacasse and Magnan (1992): the importance of littoral habitats (0-2 m depth), which was assessed using visual indices determined by two observers from a boat; the importance of macrophytes and submersed wood, estimated using an index ranging from 0 and 5; the importance of other refuge habitats such as emergent vegetation, bushes, and semisubmersed wood, which was evaluated by multiplying their percent of littoral occupation by an index of refuge quality ranging from 1 to 10; the percent littoral occupation was estimated linearly between two landmarks on a series of transects covering the entire shoreline, except for lakes larger than 100 ha for which the observations were done on one third of the shoreline; and the percent littoral occupation of open habitats (rocks, rock outcrops, beaches, and mud flats).

Statistical Analysis

To describe the structure of interindividual variation in the diet of brook charr, we plotted the frequency of individuals against the percent weight of benthic organisms found in their stomach (the preferred prey of brook charr in allopatry; see references above). As the charr feed mainly in two habitats, the littoral zone (on benthic prey) and the pelagic zone (on zooplankton, dipteran pupae, swimming insects, terrestrial insects and prey fish), we do not present these plots for pelagic prey because they always represent the complement of the percent weight of benthic prey.

We examined how the level of interindividual variation was related to the average proportion of benthic or pelagic food consumed in a lake by plotting the standard deviation of the percent weight of benthic prey versus the mean percent weight of benthic prey (mean and SD calculated across all individuals in each lake). Lakes with a very low or very high mean percentage of benthic prey must contain mostly benthic or pelagic "specialists" and therefore have little interindividual variation, as reflected by a low SD. Examination of the overall shape of the SD vs mean curve indicates how the transition takes place between lakes containing mostly benthic specialists and those dominated by pelagic specialists. For example, this curve should be relatively flat (constant SD) if lakes with intermediate levels of benthic prey consumption contain mostly generalists, but it should be dome-shaped (high SD near the center, low SD at the extremes) if these lakes contain a mixture of benthic and pelagic specialists, with very few or no generalists.

Stepwise multiple linear regressions were used to quantify the effects of the determinants of diet specialization (forward selection procedure in SPSS X.2). We defined the percent of individuals having more than 90% of benthic prey in their stomach (benthic specialists) as the dependent variable. One model was built with all the samples. In this case, we used those independent variables that were available in all of the seven previous studies. Other models were built for each data set separately because some of the independent variables (physicochemistry, thermal habitat, littoral habitat structure) were

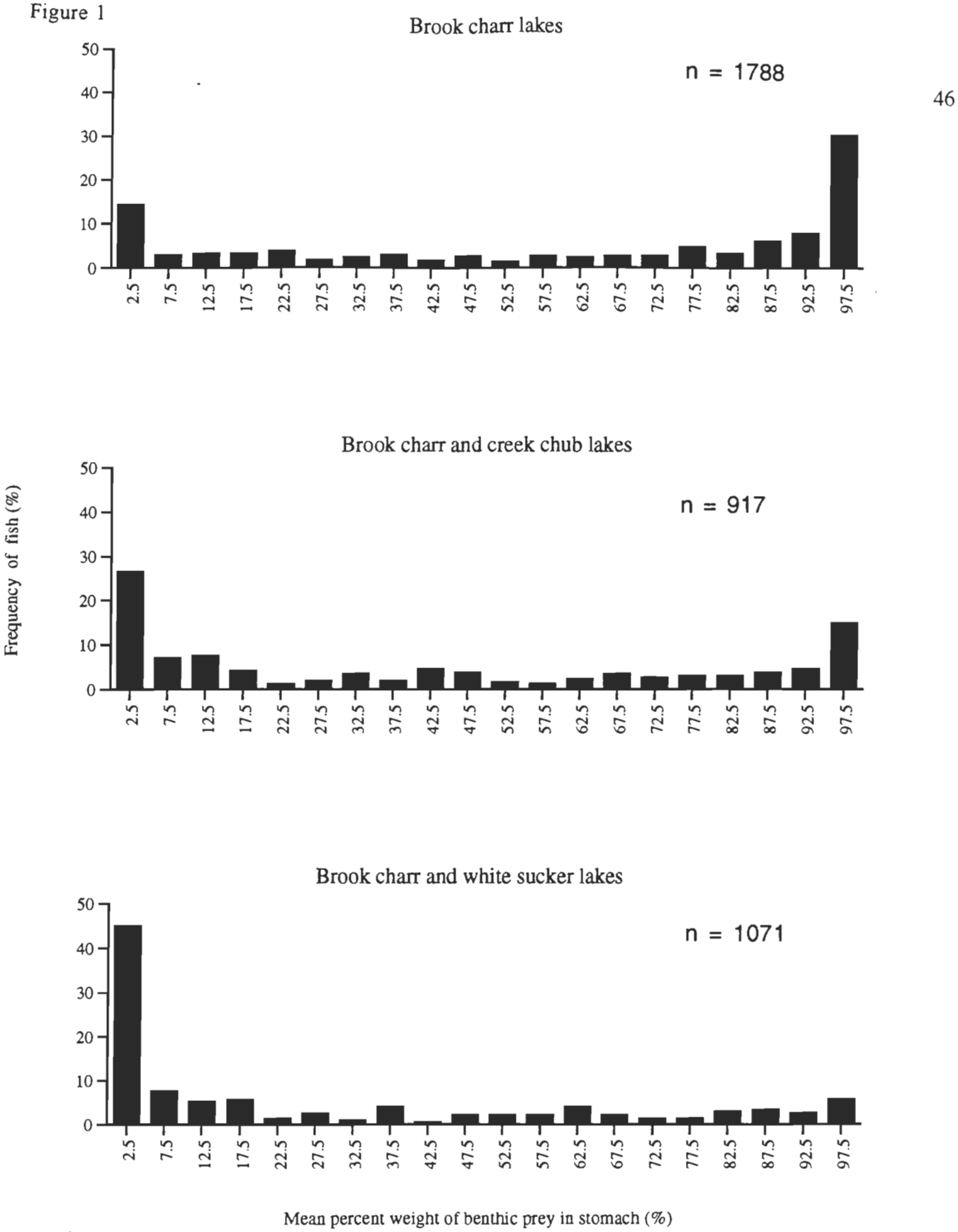
specific to individual studies. The best models were selected on the basis of their R^2 values and the mean square error associated with the estimate. Collinearity between the independent variables was evaluated by examination of the pairwise correlation coefficients. The SPSS X.2 regression procedure also uses the "tolerance and minimum tolerance tests" to prevent collinearity problems (Tabachnick and Fidell 1983). When collinearity occured, each collinear variable was used to build a separate model that was then compared with all of the other models. Residual scatterplots, normal probability plots (Tabachnick and Fidell 1983), and partial residual plots (Larsen and McCleary 1972) were used to determine if the assumptions of the multiple linear regression were satisfied (i.e. normality, linearity, and homoscedasticity of residuals).

Finally, we used data on the abundance of 8 benthic prey categories in the stomachs of benthic specialists (10 individuals captured in different location of the littoral zone of Lake Vautour on 19 June 1985; Tremblay and Magnan, 1991), to evaluate the interindividual variation in diet within a single habitat (here the littoral zone). Shannon diversities were computed to quantify these variations. The low number of zooplankton taxa precluded a similar comparison for the pelagic habitat.

Results and Discussion

Although analyses on frequency distributions were done for each data set separately, only those effected on pooled samples are presented because the patterns were similar (see Bourke 1996 for presentation of separate samples). The results show a great within-population variability in the diet of brook charr (Figure 1). Some of the charr had fed almost exclusively on benthic organisms (mean percent weight of benthic prey > 90%; benthic specialists), others, almost exclusively on pelagic prey (mean percent weight of benthic prey < 10%; pelagic specialists), the rest being "generalists" (mean percent weight of benthic prey between 10% and 90%). These results indicate that charr populations in the study lakes were not composed by an ensemble of generalist individuals with regard to

Figure 1


Brook charr lakes
n = 1788
Brook charr and creek chub lakes
n = 917
Brook charr and white sucker lakes
n = 1071
Frequency of fish (%)
0
10
20
30
40
50
2.5
7.5
12.5
17.5
22.5
27.5
32.5
37.5
42.5
47.5
52.5
57.5
62.5
67.5
72.5
77.5
82.5
87.5
92.5
97.5
Mean percent weight of benthic prey in stomach (%)

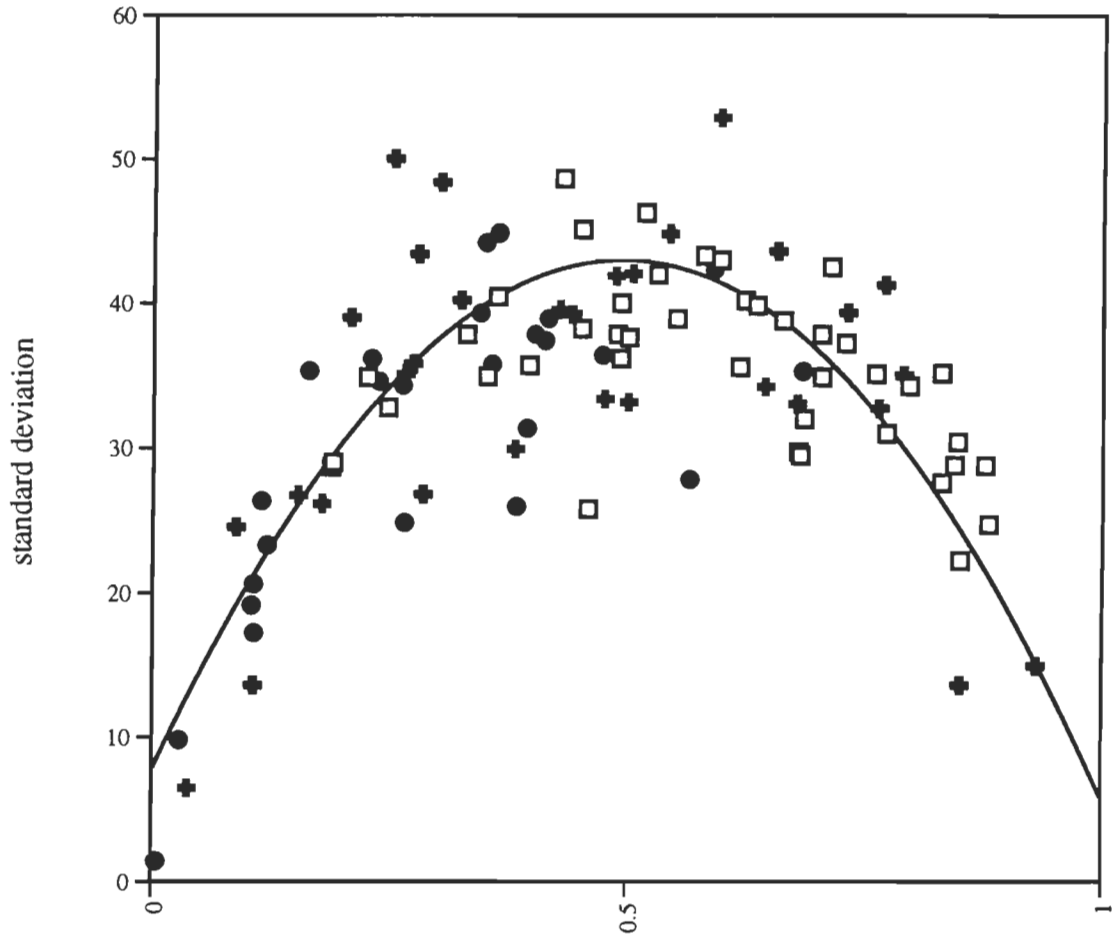
feeding habits, but rather by a combination of benthic and pelagic specialists in varying proportions, with a minor contribution by generalists. These results also support the conclusion of Bourke et al. (summitted), who found that brook charr can be divided into two groups of specialists (benthic and pelagic) and a group of generalists based on their spatial distribution, as determined by radio-telemetry in lakes of the same system. In that study, the observed interindividual differences in habitat preference were related to differences in morphology and coloration; the pectoral fins of benthic and generalist individuals were significantly longer than those of pelagic ones, and the integument coloration of benthic and generalist individuals was silver-grey while that of pelagic individuals was red (Bourke et al. submitted). Pectoral fin length and coloration appear to be related to diet. Long pectoral fins are related to the slow and precise manoeuvring (Gatz 1979; Webb 1984) required for feeding on benthic organisms on the bottom, while shorter pectoral fins are associated with cruising, which is necessary for searching efficiently in the open water habitat (Ehlinger 1990). In fish, a red coloration is mainly due to carotenoid pigments (Brush and Reisman 1965; Fujii 1993). Carotenoids cannot be synthesized by fish and must be acquired through the diet (Fujii 1993). If the spatial distribution of pelagic individuals is indeed correlated with a rich zooplankton diet, their red coloration suggests that there is a high carotenoid content in these pelagic prey. *Holopedium,* a cladoceran prey usually found in stomach contents of brook charr (Tremblay and Magnan 1991), were reddish in samples collected recently in these study lakes (P. East and P. Magnan, personal observation), suggesting the presence of carotenoids in *Holopedium.* These findings support the relationship between spatial distribution and diet in brook charr (Tremblay and Magnan 1991).

The analysis of stomach content data also showed considerable interindividual variation in the diet of brook charr among fish communities (i.e. brook charr, brook charr and creek chub, and brook charr and white sucker lakes; Figure 1); the proportion of benthic specialists decreased from 41.3% in allopatry to 19.7% in sympatry with creek

chub, and to 9.9% in sympatry with white sucker. It is remarkable that the proportion of generalist individuals was virtually the same among the fish communities (Figure 1). In this context, the niche shift of sympatric brook charr from benthic organisms to pelagic prey is not the result of increased consumption of pelagic prey by most individuals of the population (i.e. an increase in the proportion of individuals behaving as generalists), but rather of a decrease in the proportion of benthic specialist relative to that of pelagic specialists (Figure 1). This relationship indicates that interindividual variability in diet is low in allopatry, because most individuals are benthic specialists, and in sympatry with white sucker, because most individuals are pelagic specialists. In contrast, interindividual variability is highest in sympatry with creek chub, because there are high proportions of both benthic and pelagic specialists in the population. This interpretation is supported by the dome-shaped relationship between the standard deviation of the percent weight of benthic prey and the mean percent weight of benthic prey ($Y = 9.41 + 123.56X - 121.42X^2$, $R^2 = 0.61$, $p < 0.05$ (Figure 2)). These results are consistent with the conclusions of Magnan (1988) and Lacasse and Magnan (1992) who found that white sucker had a greater impact than creek chub on the niche shift of brook charr from benthic organisms to pelagic prey.

It was suggested earlier that sympatric brook charr shift to pelagic prey because chub and sucker are morphologically and behaviourally better adapted than charr to feed on bottom prey (Magnan 1988; 1989; Tremblay and Magnan 1991); the feeding apparatus of creek chub (mouth in subterminal position and protrusible premaxillae) and white sucker (mouth protrusible and in inferior position) should allow them to use bottom prey more efficiently than brook charr, whose mouth is in a terminal position. Generally, fish with a bottom-oriented mouth, or with adaptations permitting to orient the mouth downward (such as protrusible premaxillae), are more efficient when feeding on benthic prey, while fish with terminal mouths are more efficient at capturing surface and mid-water prey (Schultz and Northcote 1972; Gatz 1979; McComas and Drenner 1982; Paine et al. 1982; Magnan and FitzGerald 1984; Tremblay and Magnan 1991). From a feeding behavior perspective, creek

Figure 2


60
50
40
30
20
10
0
standard deviation
0
0.5
1
mean percent weight of benthic prey

chub and white sucker are better able than brook charr to exploit hidden and patchy benthic prey. For creek chub, laboratory experiments have shown that searching efficiency of an individual feeding in a group was improved through social facilitation (Magnan and FitzGerald 1984). Such a feeding strategy would be advantageous for species that feed on patchy, widely dispersed, and unpredictable food resources (Morse 1977; Bertram 1978), such as benthic invertebrates in temperate lakes (see Wetzel 1983). In contrast, the high level of intraspecific aggression observed in brook charr prevents the formation of such feeding groups (see Magnan and FitzGerald 1984; East and Magnan 1987). Also, it was observed that the size distribution of benthic prey consumed by white sucker was similar to that of benthic invertebrates in the substratum (Tremblay and Magnan 1991). In contrast, brook charr consumed the largest benthic prey available both in sympatry and in allopatry, presumably because they select their prey one by one according to size. Therefore, the feeding behavior of white sucker leaves very few possibilities for brook charr to take competitive refuge on the benthic prey size axis, in terms of limiting similarity (MacArthur and Levins 1967; MacArthur 1972; Roughgarden 1974; Werner 1977). It is probably for this same reason that the white sucker has a greater impact than creek chub on the niche shift of brook charr from benthic to pelagic prey. In contrast to white sucker, creek chub are gape-limited on the benthic prey size axis, which leaves more space for brook charr to feed on larger prey.

Determinants of the specialization

High correlations (r = 0.70-0.99) were found between lake area, volume, shoreline length, littoral area, island area, thermal habitat area, and thermal habitat volume, between maximum depth, mean depth, volume, and thermal habitat volume, and between refuge and open habitat importance. These independent variables were not considered simultaneously in regression analyses.

When all samples were considered together, the best predictor of the proportion of benthic specialists was the presence of white sucker (negatively correleted: -), which accounted for 18% of the variation (Table 1). Maximum depth (-) contributed an additional 3.2% of this variation. Independent variables explained up to 75% of the variation when models were built for each data set separately (Table 1). For charr larger than 200 mm total length, white sucker explained 28.5%, 35.2%, and 37.9% of the variation (-) of the proportion of benthic specialists in the studies of Magnan (1988), Tremblay and Magnan (1991), and Lacasse and Magnan (1991), respectively (Table 1). The creek chub (-) and lake mean depth (-) contributed respectively to 25.7% and 14.5% of this variation in the study of East and Magnan (1991), who investigated only brook charr and brook charr and creek chub lakes (Table 1). Many authors have reported a negative relationship between mean depth and zoobenthos abundance or production (Rawson 1955; Johnson 1974; Hanson and Peters 1984; Plante and Downing 1989). In lakes with low mean depth, brook charr appeared to experience a lower competitive pressure from creek chub and white sucker, possibly because benthic resources are more abundant in such lakes. The creek chub explained a significant portion of the variation in the dependent variable only in the data set dealing with brook charr and brook charr and creek chub lakes (East and Magnan 1991). This supports the observation that white sucker has a greater impact than creek chub on diet of brook charr; when brook charr and white sucker lakes are included in a data set, the creek chub is never a determinant of the brook charr diet.

Two of the seven data sets considered in this study included charr smaller than 200 mm TL (Tremblay and Magnan 1991; Venne and Magnan 1995). Models built with these data sets report on the importance of the variable month (May to September) as a predictor of the proportion of the mean percent of benthic prey in the diet (Table 1). This independent variable explained 73.4% of the variation (-) in the study of Tremblay and Magnan (1991) and 24.2% in the study of Venne and Magnan (1995). Here, the observed decline in the proportion of benthic specialists during the summer could be due to the

Table 1. Best models predicting the proportion of individual with more than 90% of benthic prey in their stomach. The probability (p) associated with each independent variable, the standard error of the coefficients (SE), the partial R^2 associated with each variable[a], the adjusted R^2, and the standard error of the estimate (S_{xy}) are also listed.

Model	$p > t$	SE	R^2	adj R^2	S_{xy}
% of fish with benthos > 90%					
All studies			21.2	19.9	21.7
- 23.0 white sucker[b]	0.001	4.1	18.0		
- 0.5 max depth	0.028	0.2	3.2		
<u>charr > 200 mm</u>					
Magnan (1988) (17 lakes)			28.5	23.7	20.8
- 27.1 white sucker	0.027	11.1	28.5		
Lacasse and Magnan (1992) (42 lakes)			37.9	36.1	18.6
- 30.0 white sucker	0.001	6.6	37.9		
East and Magnan (1992) (24 lakes)			40.2	34.8	22.9
- 34.9 creek chub	0.002	9.7	25.7		
- 3.5 mean depth	0.030	1.5	14.5		
Tremblay and Magnan (1991) (2 lakes)			35.2	29.3	13.4
- 18.2 white sucker	0.033	7.4	35.2		
<u>charr < 200 mm</u>					
Tremblay and Magnan (1991) (2 lakes)			73.4	70.1	16.0
- 21.4 month	0.002	4.5	73.4		
Venne and Magnan (1995) (6 lakes)			74.9	67.7	9.2
- 1.4 lake area	0.012	0.4	50.6		
- 8.1 month	0.036	3.1	24.2		

[a]Calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1983).

[b]negative (-) or positive (+) correlation together with regression coefficient and selected indep. var.

seasonal decline of zoobenthic biomass which occurs in temperate lakes through summer (Mittlebach 1981; Persson 1987; Tremblay and Magnan 1991). This could also be related to the thermal constraints associated with the littoral habitat during the summer months; the thermal preferendum of brook charr is 15.4°C (Wismer and Christie 1987) and the temperature of the littoral habitat can reach up to 20°C during this period (see Tremblay and Magnan 1991). Lake area (-) explained 50.6% of the variation in the proportion of benthic specialists (<200 mm TL) in the study of Venne and Magnan (1995). As lake area is correlated with mean and maximum depth (r^2=0.56 and 0.64), it is possible that the abundance and production of zoobenthos are higher in these lakes, explaining why the proportion of benthic specialists is inversely related to this variable.

Within habitat variability

There was also a great individual variability in the diet of benthic specialists collected in the littoral zone (Table 2). Ephemeroptera larvae were the most important prey found in the stomach contents of nine of the ten individuals studied. However, while Ephemeroptera larvae accounted for more than 80% of the stomach contents (by weight) for some individuals, they represented between 0 and 30% for others. Differences among individuals were also found for the seven other benthic prey categories (Table 2), and were illustrated by the variation in the Shannon diversity index (0.00 to 0.99). These results in addition to the individual variation in the diet of brook charr observed between habitats, there is an important within-habitat individual variability. In a mark-recapture experiment, Bryan and Larkin (1972) also observed that individual fish utilized only a part of the entire spectrum of prey types consumed by all individuals in the same habitat. In our study, it is difficult to evaluate if these differences are related to food preference, feeding efficiency for particular prey items, or are only related to the patchy distribution of prey in the littoral habitat. In fact, the analysis of stomach content data usually generates the suspicion that individual fish do tend to have what appear to be different searching techniques or different

Table 2. Mean percent weight of eight benthic prey categories in the stomach of 10 brook charr (with more than 90% of benthos in their stomach) captured on 19 june 1985 in lake Vautour (Tremblay and Magnan 1991). Shannon diversity index are also listed for each fish.

No	Diptera	Trichoptera	Ephemeroptera	Odonata	Chironomid	Sialidea	Gammaridea	Other benthic organisms	Shannon diversity index
1	0.00	12.03	0.00	87.97	0.00	0.00	0.00	0.00	0.17
2	0.00	0.00	24.77	24.95	0.00	23.01	0.00	27.27	0.65
3	0.00	0.00	85.77	0.00	11.49	0.00	2.74	0.00	0.22
4	0.14	0.00	27.86	0.00	0.39	0.00	0.00	71.61	0.29
5	0.00	8.27	91.73	0.00	0.00	0.00	0.00	0.00	0.13
6	0.00	0.00	84.26	0.00	0.00	15.74	0.00	0.00	0.20
7	2.13	0.00	96.60	0.00	1.27	0.00	0.00	0.00	0.07
8	0.00	0.00	91.30	0.00	0.00	0.00	8.70	0.00	0.13
9	0.00	2.95	56.79	40.26	0.00	0.00	0.00	0.00	0.37
10	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00

"tastes", but the evidence is characteristically circumstantial. Only data on the food of the same individual at different times can clearly demonstrate these phenomena (Bryan and Larkin 1972). In our study, this is true for the within-habitat interindividual variation.

In conclusion, the interindividual variation in the diet of brook charr observed among habitats is supported by three different facts: (1) the analyses were based on 3776 individual distributed over 70 lakes, seven years, five summer months, and two size classes, and thus should be representative of a general pattern, (2) individual segregation in diet is correlated with individual segregation in habitat use, where benthic, pelagic and generalist individuals were identified through radio-telemetry during summer periods lasting 2-3 months in the same system (Bourke et al. summitted), (3) the proportion of benthic, pelagic, and generalists individuals in the present study (based on diet) fits remarkably well with that in Bourke et al. (summitted), based on spatial distribution ; and (4) individual specialization in habitat use was supported by functional relationships between diet and morphological traits such as pectoral fin length and coloration pattern (Bourke et al. summitted).

As mentioned earlier, the brook charr is considered to be a generalist carnivorous species that uses both the pelagic and littoral habitats in the study lakes. The results of this study provide evidence that lacustrine brook charr populations are not composed of a collection of similar generalists, but rather by a mixture of benthic and pelagic specialists, with a minor fraction of generalist individuals. The population can be classified as generalist but not most individual fish. This kind of subdivision presumably allows habitats to support higher population densities than if all individuals were generalists, and thus promotes population persistence under marginal conditions (Morse 1980).

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Figure captions

Fig.1. Frequency of individuals in relation to the percentage of benthic prey in their stomach for brook charr lakes, brook charr and creek chub lakes, and brook charr and white sucker lakes. The number of stomach contents analysed appears at the top of each figure.

Fig.2. Relationship between the standard deviation of the percent weight of benthic prey and the mean percent weight of benthic prey (mean and SD calculated across all individuals in each lake). The fitted curve corresponds to the equation $Y = 9.41 + 123.56X - 121.42X^2$. Square: brook charr lakes, cross: brook charr and creek chub lakes, circle: brook charr and white sucker lakes.

CHAPITRE 3

Diel locomotor activity of brook charr, as determined by radio-telemetry

Abstract. Localizations by radio-telemetry during 8 - 24h sampling periods in 1991, 1992, and 1993 were used to evaluate the diel activity patterns of adult brook charr (*Salvelinus fontinalis*) in two lakes (de l'Épervier and Ledoux) of the Laurentian Shield (Québec, Canada). Based on the "minimum travelled distance" between two consecutive localizations, adult brook charr were more active at dusk and at night than during the day. During daylight periods, individual fish displayed strong site selection, remaining in the same area along the shore from day to day. The fish left their inshore position at dusk, were highly mobile during the night, and then returned to their focal point at sunrise, exhibiting diel homing behaviour. These results are supported by a nightime increase in gillnet captures of adult brook charr in a small lake (Melchior) of the same area. Data obtained by gillnet fishing in two other lakes (Bondi and Simpson) showed that juvenile (1+) brook charr were active throughout the diel cycle and young-of-the-year were active mainly during the day, suggesting an ontogenetic change in the diel activity of brook charr. Despite its limitations (restrictions in the number and size of tracked individuals, post-manipulation mortality, and duration of the tracking period), radio-telemetry allows for collection of multiple observations of individual fish behavior during their activity cycle, such as travelled distances, instantaneous activity, site selection and homing, and thus provides more detailed informations on spatial distribution than alternative methods such as gillnetting.

INTRODUCTION

Salmonids are often characterised as diurnally active fish (see Linner *et al.*, 1990). However, some of our preliminary observations suggested a nocturnal activity pattern in lacustrine adult brook charr, *Salvelinus fontinalis* (Mitchill). Although the activity patterns of anadromous (White, 1941; Smith & Saunders, 1958; Castonguay *et al.*, 1982; Doyon *et al.*, 1991) and stream-dwelling brook charr (Griffith, 1974; McNicol *et al.*, 1985; Grant & Noakes, 1987; Walsh *et al.*, 1988; McLaughlin *et al,*. 1994) have been studied often, little is known on lacustrine populations. The purpose of this study was (1) to evaluate the diel locomotor activity pattern of adult brook charr in two lakes using radio-telemetry, (2) to compare these results with those obtained by gill net fishing in the same system, and (3) to compare diel activity patterns of adult brook charr to those of young-of-the-year (YOY) and juveniles.

STUDY LAKES

Brook charr were tracked by radio-telemetry in Lakes de l'Épervier (1991) and Ledoux (1992, 1993) located in the Mastigouche Reserve (46°38'N, 73°15'W); gill net samples were collected in Lakes Bondi (1993) and Simpson (1992) in the same Reserve, and in Lake Melchior (1979), located in the St-Maurice Reserve (47°05'N, 73°20'W), in Québec (Canada). The lakes are small and typical of oligotrophic temperate zone lakes with respect to surface area, depth, conductivity, dissolved oxygen, thermal stratification, and Secchi disk transparency (see Magnan & FitzGerald, 1982, Magnan, 1988, Lacasse & Magnan, 1992; Table I). Lake Melchior contains only brook charr while Lakes Bondi, de l'Épervier, Ledoux, and Simpson contain brook charr and northern redbelly dace, *Phoxinus eos* (Cope). The five lakes are subject to sportfishing, and exploitation is carefully controlled by the Québec Government (see Magnan, 1988). The lakes were closed to sportfishing during the study.

Table I. General characteristics of the study lakes.

Lake	Year	Area (ha)	Mean depth (m)	Conductivity (µS/cm)	Secchi disk (m)
Melchior	1979	5.2	4.6	-	6.1
Simpson	1992	28.5	3.3	12.5	2.5
Bondi	1993	23.3	8.0	10.5	3.5
Épervier	1991	8.4	5.6	14.1	3.5
Ledoux	1992-1993	11.9	5.5	15.3	4.2

MATERIALS AND METHODS

MARKING

In June or July of each summer (Table II), 20 adult brook charr (250-419 mm total length) in lakes de l'Épervier and Ledoux were tagged with thermosensitive radio-transmitters weighing 4g (Advanced Telemetry Systems, ATS, model 357). Based on the study of Magnan & FitzGerald (1982) in the same system, these fish were 3 years of age or older. Fish were captured with experimental multifilament gillnets (1.8 m deep by 38.1 m long, with stretched meshes of 2.5, 3.8, 6.4, and 7.6 cm) arbitrarily set perpendicularly to the shore, mainly in the littoral zone. Gillnets were removed every 15 minutes and only fish in good condition, usually those caught by the teeth, were retained for marking.

Transmitters were attached externally under the dorsal fin after the fish were lightly anaesthetized with tricaine methanesulphonate (MS-222). Fixation was made with nylon monofilament threaded through muscular tissues at two points. The transmitter was placed on one side of the fish while on the other side the filament and fixation knot were kept apart from the fish by a small rubber plate (Winter, 1983). A neoprene cushion was placed between the fish and the rubber plate to avoid lesions due to rubbing on teguments. In 1991 (Lake de l'Épervier) the fish were kept for 2h in a holding enclosure (littoral zone) before release into the lake. A total of four fish survived to these manipulations in 1991 (Lake de l'Épervier) compared to 11 in 1992 and 14 in 1993 (Lake Ledoux). In 1991, longer manipulations and holding periods in the enclosure were probably more stressful for the fish and thus were responsible for the higher observed mortality. In 1992 and 1993, manipulation time was much reduced by using a cone-shaped needle rendering thread insertion easier, and by eliminating the post-operatory holding period. Colder water than in 1991 was used in the manipulation basin. The tagging process generally lasted less than one minute per fish. In each of the three years, most of the mortality occurred during the 10 days following marking. All of the fish that were alive after 10 days were tracked until the transmitter batteries were exhausted. Periods of tracking are shown in Table II.

Table II. Mean fork length of brook charr tracked by telemetry and periods of fish localizations.

Lake	Year	n[1]	Mean total length (mm)	S.D.	Range (mm)	Sampling period
Épervier	1991	4	341	18	325-360	29 June - 29 August
Ledoux	1992	11	343	45	250-400	21 July - 30 October
Ledoux	1993	14	387	30	320-419	22 July - 28 October

1. Number of fish tracked.

FISH LOCALIZATION

Localization of individual brook charr was done on average every two days during each sampling period (Table II) using an ATS-R2000 radio receiver equipped with a loop antenna. At every visit, each fish was localized during the daylight period (8:00 to 18:00) by triangulation, using a compass and landmarks spaced regularly around the lakes. The water temperature measured by the thermo-sensitive tag (hereafter ambient temperature) was noted at four different occasions: when each fish was localized (to determine their vertical position according to the thermal profile of the lake on a given sampling date), and at the beginning, middle, and end of the period in which all individuals were localized, which lasted around 2h in 1991 and 4h to 6h in 1992 and 1993. On each sampling sampling date, the ambient temperature of a given fish was calculated as the mean of the 4 measurements. At each fish localization the lake depth was determined also with a graduated cord to position the individuals more accurately on the bathymetric map.

On three occasions in 1991 and 1992 and two occasions in 1993, fish were localized every 4h during complete 24h cycles. Thus, for a given cycle, four to seven fish were localized at 10h, 14h, 18h, 22h, 2h, and 6h to evaluate their diel locomotor activity pattern.

GILL NET FISHING

To examine the diel locomotor activity pattern of adult brook charr (2+, 3+) using gill net fishing, two stations were established in Lake Melchior. At one station, situated in the littoral zone (2m), an experimental multifilament gill net (1.8 m deep and 38.1 m long with stretched meshes of 2.5, 3.8, 5.1, 6.4, and 7.6 cm) was placed parallel to the shore. At the second station, situated in the offshore zone (6-8 m of water), five multifilament gill nets were suspended vertically in the water column. These nets (1.8 m wide and 8 m long) each with one mesh size as above, were horizontally spaced at 1-m intervals. On three sampling periods in 1979 (June, July, and August), the number of charr (217 ± 26 mm fork

length) and their position in the water column was recorded every 4h during a complete 24h cycle.

In the course of two other studies (Héroux & Magnan; Dynes & Magnan, unpublished data) we obtained data on the diel locomotor activity of YOY (0+) and juvenile (1+) brook charr. In Lake Simpson, juvenile brook charr (106 to 188 mm total length, TL) were captured in the littoral zone with 5 multifilament gill nets (1.5 m in height and 30 m long with stretched mesh of 2.5 cm) at 3 h intervals starting at 15:00h on 10 June 1992 and continuing for 48 h. The nets were never left more than 60 minutes in the water (mean ± SD: 37 ± 8 min.). In Lake Bondi, YOY brook charr (60.0 ± 4.5 mm TL) were also captured in the littoral zone at 8h, 12h, 16h, and 20h. Gill nets (1.8 m in height and 14.5 or 29.0 m long with stretched mesh of 1.25 cm) were set perpendicularly to the shore at eight sampling stations around the lake for periods of 4h. Althought no information is available for the sampling periods of 24h and 4h, these data will be used here to support information found in the literature on daytime activity.

STATISTICAL ANALYSES

To evaluate the diel locomotor activity pattern of adult brook charr using radio-telemetry, two different measures of displacement were used for all fish tracked during the eight 24h sampling periods. First, the "minimum travelled distance" which represents the linear distance (m) between two consecutive localizations, irrespective of the total length of the actual trajectory of the fish between these two points. Five measures of "minimum travelled distance" were obtained for each fish, one for each interval of the diel cycle (i.e. 10-14h, 14-18h, 18-22h, 22-2h and 2-6h). The localizations indicated that on a day-to-day basis individual fish tended to be very faithful to a given site during the daylight period (see Results, section). Thus, for each fish a "focal point" corresponding to the middle point of its overall daily localization (10:00-18:00h) during the summer was calculated. To investigate the diel locomotor activity of brook charr in relation to the focal point, the mean

distance of all tracked individuals from their focal point was compared among the different periods of the day. In this context the "minimum travelled distance" gives information about the extent of the movement between two consecutive localizations, with no reference to fixed spatial coordinates, while the "distance from focal point" describes the displacement from the focal point in relation to the time of the day. The mean ambient temperature of all tracked individuals was also compared among the different periods of the day, for each diel sampling period.

To quantitatively evaluate the diel locomotor activity pattern of brook charr using gill net fishing, the frequency distribution of the number of fish captured was compared among the different periods of the day, for each of the 24h sampling periods in Lakes Melchior, Simpson, and Bondi.

RESULTS

DIEL LOCOMOTOR ACTIVITY

Radio-telemetry. Based on the "minimum travelled distance" between two consecutive localizations, adult brook charr were more active at dusk and at night than during the day (Table III). During daylight periods, individual fish displayed strong site selection, remaining in the same restricted area along the shore from day to day (Table IV). The sites selected by the fish were located in the same part of the lake for almost all individuals (Figure 1). Fish movement was restricted in daytime relative to the distances travelled at dusk and night (Figure 2). The typical pattern of diel movement is illustrated in Figure 3, in which two fish leave their inshore position at dusk, are highly mobile during the night, and then return to their focal point at sunrise.

Gillnet fishing. With the exception of the 24:00 and 4:00h sampling periods for which no data are available, YOY brook charr (0+) were mainly active between 10:00 and 18:00h (Figure 4, A). The juveniles (1+) were active in all sampling periods (Figure 4, B), and adults (2+, 3+) were mainly active between 18:00 and 2:00h (Figure 4, C). As observed

Table III. Minimum distance travelled between two consecutive localizations during different periods of the day, for all fish tracked in the present study.

Period	n[1]	Movement (m)	S.D.
10:00 to 14:00	29	42.8	78.2
14:00 to 18:00	29	45.0	68.5
18:00 to 22:00	29	108.9	71.5
22:00 to 2:00	29	104.4	91.4
2:00 to 6:00	29	109.8	91.4

1. Number of localizations

Table IV. Mean distance of each fish from their focal point during daylight localizations (10:00 to 18:00 h).

n[1]	Mean distance (m)	S.D.
21	24.9	20.1
16	30.5	26.1
21	31.5	22.9
21	29.4	29.2
16	29.0	26.9
21	31.8	41.2
21	13.6	10.4
15	20.7	14.9
16	20.3	21.1
21	16.1	10.9
16	20.3	19.1
21	21.6	17.2
16	17.2	13.7
20	18.5	16.5
16	17.9	19.5
20	15.5	13.7
16	25.4	20.9
14	21.7	23.4
20	21.0	9.5
12	21.3	23.3
20	15.0	11.8
20	24.9	24.4
20	14.3	14.0
16	21.2	23.0
16	20.9	13.3
15	19.8	16.5
13	27.3	18.8
15	22.1	18.6
15	33.8	18.6
Mean	22.3	19.3

1. Number of localizations. Each line represent an individual fish.

Figure 1

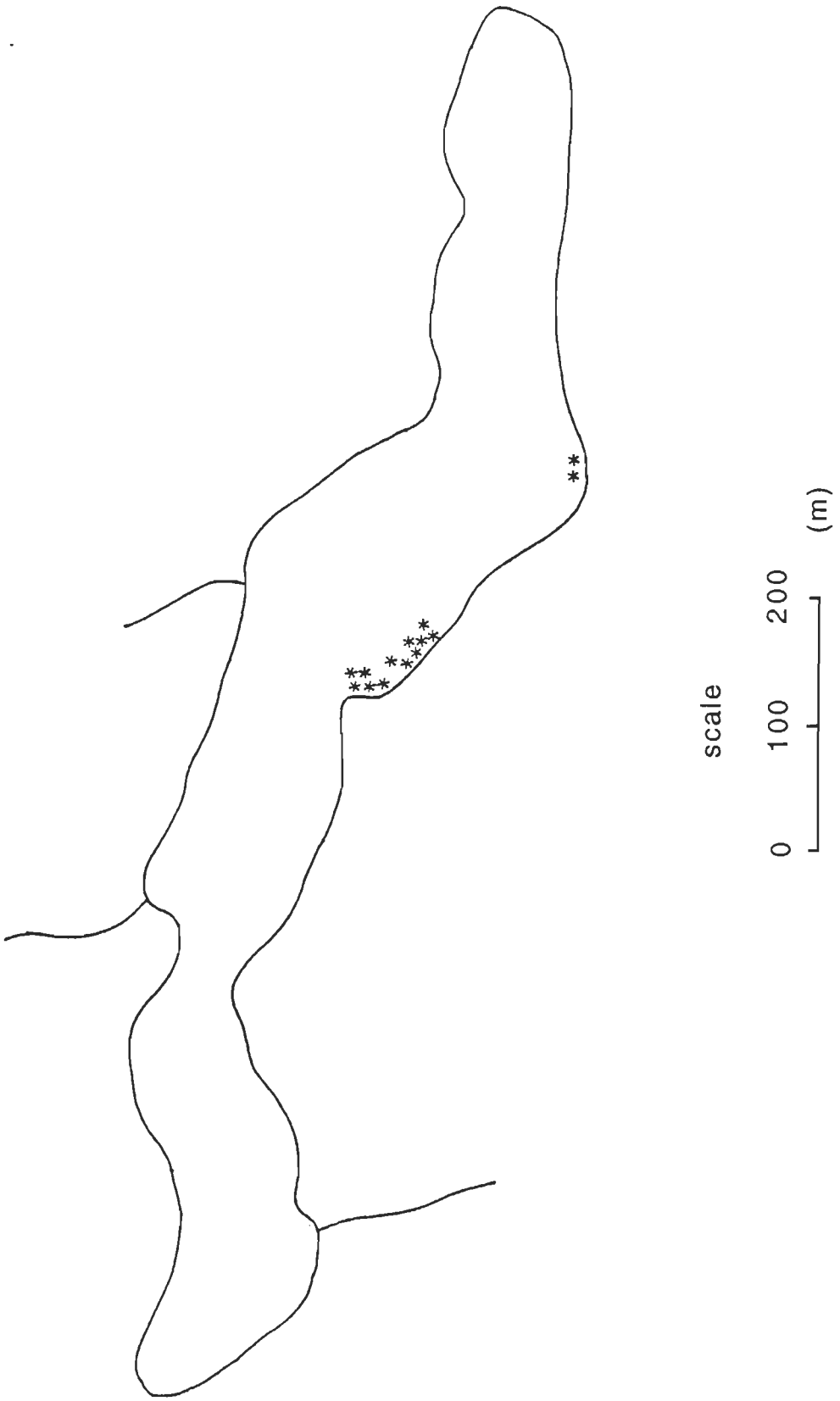


Figure 2

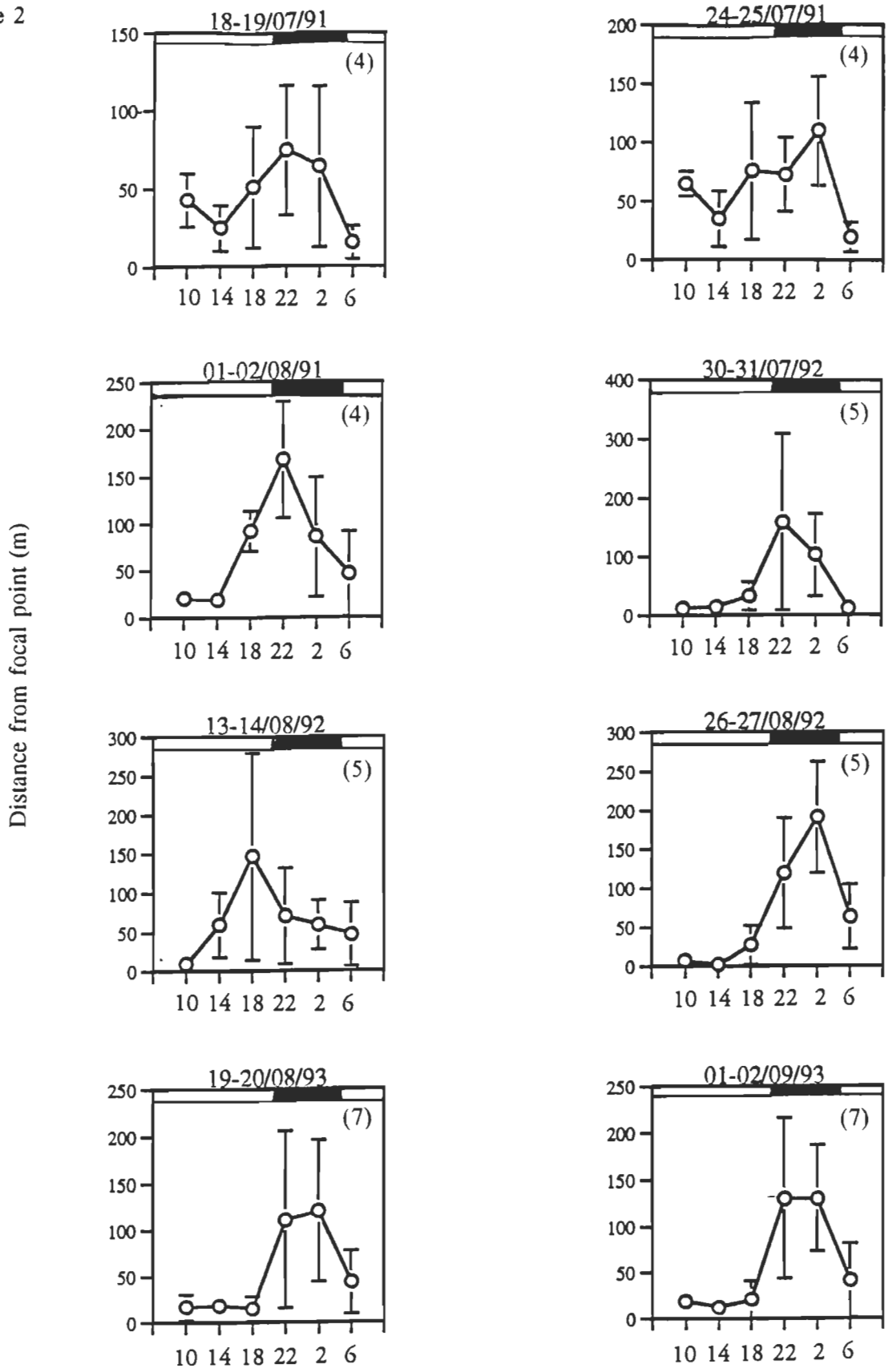
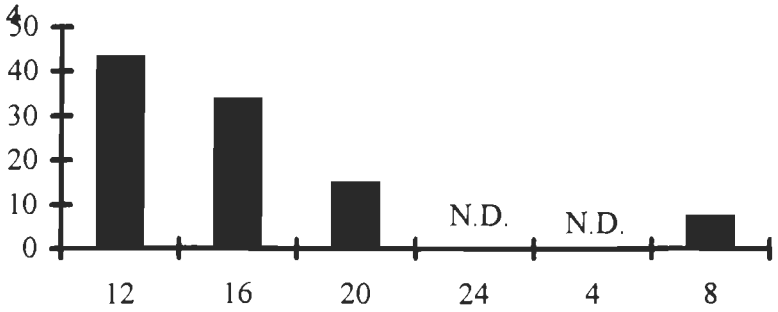

18-19/07/91
(4)
24-25/07/91
(4)
01-02/08/91
(4)
30-31/07/92
(5)
13-14/08/92
(5)
26-27/08/92
(5)
19-20/08/93
(7)
01-02/09/93
(7)
10 14 18 22 2 6
Distance from focal point (m)
Hour

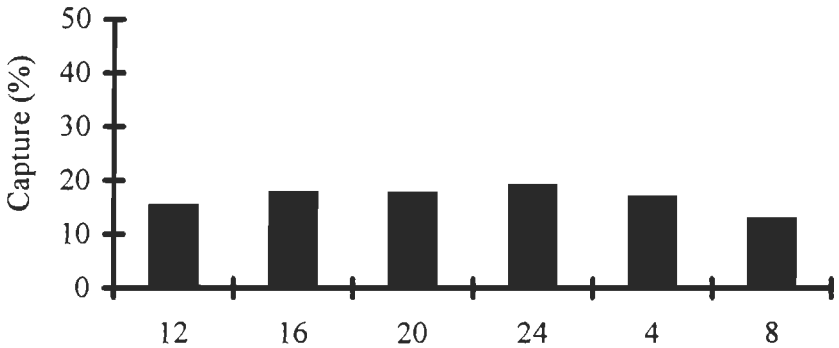
Figure 3

Figure 4

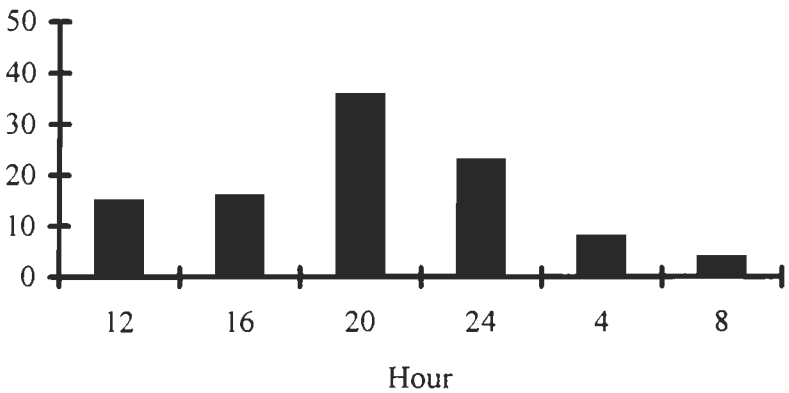
Young-of-the-year (Lake Bondi)



Juveniles (Lake Simpson)



Adults (Lake Melchior)



with telemetry, gillnet fishing in Lake Melchior also suggested higher locomotor activity for adult brook charr during dusk and around midnight (Figure 4, C).

AMBIENT TEMPERATURE

For each of the eight 24 h sampling periods, no significant difference was found in the mean temperature selected by the fish between day and night ($p>0.05$). The overall mean selected temperatures (eight cycles) was 12.3 ± 1.8°C during the day and 11.9 ± 1.2°C during the night.

DISCUSSION

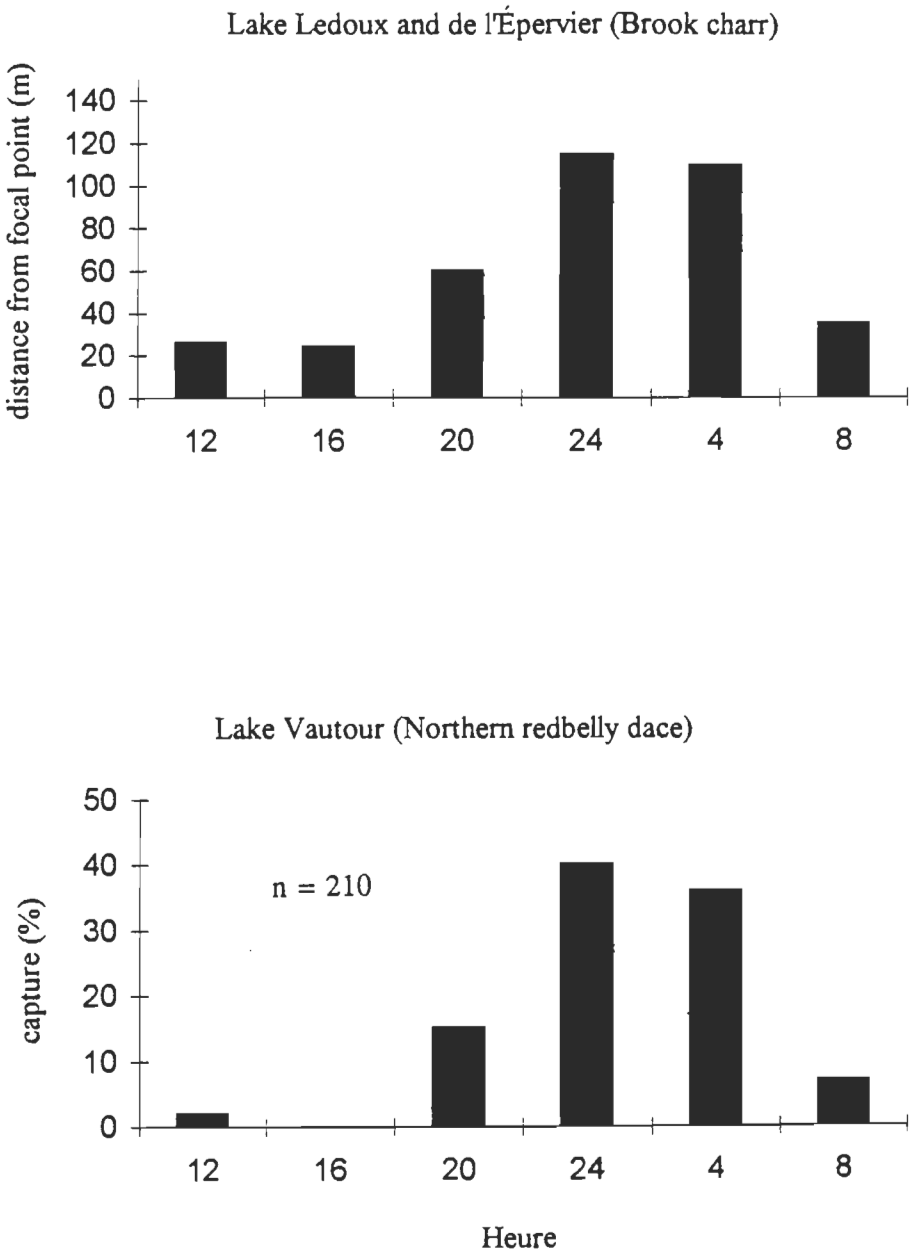
DIEL LOCOMOTOR ACTIVITY IN ADULT BROOK CHARR

The results of the present study suggest that over a 24h period, the distribution and locomotor activity of adult brook charr are divided into diurnal and nocturnal phases in the lakes. During daylight periods, brook charr were less active compared to dusk and night periods, as shown by the minimum travelled distance between two consecutive localizations. During night and dusk, the fish were also found farther from their focal point than during the day. This migration was initiated around 18:00h, and was characterized by dispersion of individuals in the lake associated with active swimming during the night. The fish then returned to their focal point, near shore soon after sunrise, exhibiting diel homing behaviour. Data obtained by gillnet fishing in Lake Melchior supported this diel locomotor activity pattern, with an increase in captures at nightime. Numerous studies have identified similar locomotor activity patterns in lakes for golden shiner *Notemigonis crysoleucas* (Mitchill) (Hall *et al.*, 1979), roach, *Rutilus rutilus* (L.), rudd, *Scardinius erythrophthalmus* (L.), bream, *Abramis brama* (L.), and bleak, *Alburnus alburnus* (L.) (Bohl, 1980), goby, *Pomatochistus pictus* (Malm) (Hesthagen, 1980), creek chub, *Semotilus atromaculatus* (Mitchill) (Magnan & FitzGerald, 1984) and walleye, *Stizostedion vitreum* (Mitchill) (Prophet *et al.*, 1989).

A question that arises is whether the diel locomotor activity of adult brook charr closely reflects their feeding pattern. Although some authors have clearly demonstrated a strong relationship between feeding and activity in fish (Elliott, 1976; Magnan & FitzGerald, 1984; Boisclair, 1992), there is some ambiguity regarding this relationship. It is often stated that if there is no activity, there will be no feeding, but also that high activity does not necessarily mean that feeding takes place. In *Alosa pseudoharengus* (Wilson), for instance, swimming activity is diurnal and feeding is nocturnal (Hesthagen, 1980). However, Boisclair (1992) identified a positive correlation between feeding (digestive tract contents; cal $30min^{-1}$) and activity (estimated by an underwater video camera system; cal $30min^{-1}$) for 0+ brook charr, and this result should apply also for adults: (1) adult brook charr should fed more actively at night to profit from a greater availability of benthic prey (e.g. Grossman *et al.*, 1980). Some invertebrates such as amphipods and chironomid pupae (Mundie, 1959), and gammarids (Grossman *et al.*, 1980) seem to be more active at night and presumably are more available to fish at that time (Magnan & FitzGerald, 1984); (2) Naud & Magnan (1987) found that northern redbelly dace, a prey of brook charr, also display diel onshore-offshore migrations. These fish swim in shoals in the littoral zone during the day, migrate at sunset to the pelagic zone, where the shoals break up, and then return to the littoral zone at sunrise (Figure 5). This movement pattern clearly agrees with that of brook charr in the present study (Figure 5). Predation on northern redbelly dace by large brook charr (TL > 250 mm) can represent up to 30% by weight of the charr's diet in the same study area (East & Magnan, 1991). Thus, predation on dace could be important in our study lakes; the total length of the 29 brook charr was > 250 mm (Table II), thus supporting the foraging hypothesis explaining the increased nocturnal activity of adult brook charr.

Behavioural thermoregulation could explain why the focal point of almost all individuals were concentrated in the same area in the lake during daylight periods. The bottom slope is steepest in this part of the lake (~ 45°). Because of thermal stratification, this could allow individuals to minimize horizontal movements between a feeding area

Figure 5


Lake Ledoux and de l'Épervier (Brook charr)
distance from focal point (m)
140
120
100
80
60
40
20
0
12
16
20
24
4
8
Lake Vautour (Northern redbelly dace)
capture (%)
50
40
30
20
10
0
n = 210
12
16
20
24
4
8
Heure

(littoral zone and upper part of the water column; see Tremblay & Magnan, 1991) and a thermal refuge area deeper in the water column. If feeding is nocturnal, as suggested above, this diurnal thermoregulation should be important because it could enhance growth by allowing the fish to completly digest the nightime meal during the day, providing a significant bioenergetic advantage (Neverman & Wurtsbaugh, 1994). As observed by Brett (1971) and suggested by Neverman & Wurtsbaugh (1994), fish residing near a thermocline would have a relatively easy time adjusting their temperature after feeding.

ONTOGENETIC CHANGE IN DIEL LOCOMOTOR ACTIVITY

Some studies have showed that YOY (0+) brook charr in lakes (Boisclair, 1992) and both YOY and juveniles (1+) in streams (Hoar, 1942; Allan, 1981; Walsh *et al.*, 1988; Forrester *et al.*, 1994) were diurnally active. Although no data were available for the nocturnal periods, YOY from Lake Bondi exhibit a peak of activity around noon while the diel locomotor activity of juveniles (1+) from Lake Simpson (Figure 4B) shows that they were active both diurnally and nocturnally. This daily activity contrasts with the adult (2+, 3+) pattern and suggests that there is an ontogenetic change in diel activity of brook charr. Two main hypotheses have been suggested to explain these ontogenetic difference: feeding efficiency and predator avoidance. For anatomical and physiological reasons, small fish could be less efficient when foraging at lower light intensities because their eyes capture less light than those of larger fish (Helfman, 1979). Developmental change in visual anatomy could allow large fish to function more effectively at lower light levels (Helfman *et al.*, 1982), thus profiting from the greater availability of benthic prey at night (Grossman *et al.*, 1980). Furthermore, as the fish grow, mouth gape increases, allowing large individuals to consume the larger prey which are often more active during the night (Helfman, 1986).

Increased nocturnal activity of adult fish could be an anti-predator strategy for smaller fish (Werner & Gilliam, 1984). Recent behavioural studies reveal that the risk of

predation is a major factor in habitat choice by fish (Werner & Hall, 1988, Turner & Mittlebach, 1990, Sandlund *et al.*, 1992). As large predatory fish are more active at night, small fish may reduce the risk of being eaten by shifting their habitat use, reducing their foraging rate, foraging distance, or movement, or changing their diel activity patterns (Turner & Mittlebach, 1990).

In conclusion, our results suggest that radio-telemetry can provide advantages over gillnetting when studying the diel locomotor activity of fish. Despite its limitations (restrictions in the number and size of tracked individuals, post-manipulation mortality, duration of tracking period), this technique allows for multiple observations of the behaviour of individual fish during their activity cycle like travelled distances, instantaneous activity, site selection and homing, and thus provides a finer degree of spatial resolution than alternative methods such as gillnetting.

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Figure captions

Figure 1. Focal points of 14 fish, as determined from all daylight localizations during summer 1993: Lake Ledoux.

Figure 2. Mean distance of tracked individuals from their focal point for different periods of the day, for each of the eight 24-h cycles in Lakes Ledoux and de l'Épervier. The date and number of individuals (in parentheses) are given on top of each figure. Dark bar indicates darkness.

Figure 3. Diel movement pattern and daylight site selection for two fish tracked in 1992, Lake Ledoux; A: area containing 90% of the daylight localizations (10:00 to 18:00 h), B and C: movement of first (B) and second (C) fish during two 24h cycles in 1992. Numbers 1 to 6 represent the position of the fish for the 10:00, 14:00, 18:00, 22:00, 2:00, and 6:00h localizations respectively.

Figure 4. Frequency distribution of captures (gillnet fishing) according to the different periods of the day; A: young-of-the-year, B: juveniles, and C: adult brook charr. N.D.: no data.

Figure 5. Locomotor activity pattern of brook charr (mean distance of all the fish from their focal point) and of northern redbelly dace (frequency distribution of captures) according to the period of the day.

CONCLUSION GÉNÉRALE

Les résultats de ce projet de maîtrise ont conduit à la rédaction de trois articles scientifiques portant sur les variations intra- et interindividuelles chez l'Omble de fontaine. En premier lieu, l'étude des variations intra-individuelles nous aura permis de mettre en lumière le patron d'activité locomoteur journalier de cette espèce, activité surtout concentrée en période nocturne chez l'adulte, et durant le jour chez les jeunes de l'année. En ce qui concerne les variations interindividuelles, le volet télémétrie nous aura aussi permis d'identifier des différences entre les individus au niveau de l'utilisation de l'habitat en identifiant deux groupes de spécialistes (littoraux et pélagiques) et un groupe de généralistes. Les préférences spatiales ont d'ailleurs pu être mises en relation avec certains traits morphologiques (taille de la nageoire pectorale, patron de coloration), avec la température ambiante, ainsi qu'avec le comportement en période de reproduction.

Selon Roese et al. (1991), la distribution spatiale des individus détermine la disponibilité des ressources auxquelles ils ont accès. Cette affirmation est supportée par nos observations lorsqu'on compare les précédents résultats avec ceux portant sur les variations interindividuelles dans l'alimentation de l'Omble de fontaine. Ainsi, on retrouve la même ségrégation des individus en trois groupes (individus benthiques, pélagiques et généralistes). Aussi, les modèles de régression linéaire multiple nous ont permis d'identifier certains déterminants de la variabilité individuelle dans l'alimentation de l'Omble de fontaine, tous directement ou indirectement reliés à l'abondance des proies benthiques (présences de compétiteurs, avancement de la saison, importance des habitats littoraux, etc).

Cette étude amène des résultats intéressants et inédits concernant la variation individuelle et permet de mieux comprendre son importance au niveau de la dynamique des populations. Qu'elles soient d'ordre génotypique ou phénotypique, les variations

individuelles peuvent avoir d'importants effets sur la dynamique des populations. Comme au niveau interspécifique, cette répartition des ressources peut permettre à la population d'atteindre un niveau plus dense, en plus d'assurer sa survie lors de conditions marginales (Morse, 1980). L'étude des mécanismes responsables de la variabilité individuelle au niveau de la morphologie et du comportement, ainsi que la validation des modèles exploitant ces différences phénotypiques entre les individus vont sûrement compter parmi les plus importantes avenues de recherche en écologie animale dans le futur.

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ANNEXE A

Résumé de l'article 1

Individual variations in habitat use and morphology
in brook charr, *Salvelinus fontinalis*

INTRODUCTION

La variabilité individuelle dans l'utilisation de l'habitat et dans l'alimentation a longtemps été ignorée et considérée comme du "bruit", ou comme une déviation autour d'une réponse optimale (Ringler, 1983; Lomnicki, 1988). Alors que la variabilité individuelle dans les habitudes alimentaires a été bien décrite par Ivlev en 1961 et Bryan & Larkin en 1972, son importance écologique en terme de répartition des ressources, de dynamique des populations et de structure des communautés, commence a peine a être reconnue (Curio, 1976; Chesson, 1978; Morse, 1980; Dill, 1983; Ringler, 1983, 1985; Ehlinger, 1990).

Il existe essentiellement deux composantes à la variabilité individuelle: la composante intra-individuelle, représentant la diversité des ressources utilisées par un seul individu, et la composante interindividuelle, qui correspond à la diversité des ressources utilisées par différents individus d'une même population (Roughgarden, 1972, 1979).

L'objectif de cette étude consiste à identifier la variation individuelle dans la distribution spatiale de l'Omble de fontaine, *Salvelinus fontinalis* (Mitchill). Les objectifs spécifiques sont de déterminer s'il existe une spécialisation individuelle dans l'utilisation de l'habitat chez l'Omble de fontaine et si tel est le cas, de déterminer si cette spécialisation peut être reliée à des différences morphologiques, à des préférences thermiques, ou encore, à la sélection de sites de reproduction.

MATÉRIEL ET MÉTHODES

Cette étude a été menée dans les lacs de L'Épervier (1991) et Ledoux (1992, 1993), situés dans la Réserve faunique Mastigouche (46°38'N, 73°15'O), Québec (Canada). Ces lacs sont représentatifs des petits lacs oligotrophes de la zone tempérée: superficie de 8.4 et 11.9 ha, profondeur moyenne de 5.6 et 5.5 m, conductivité de 18.1 et 21.3 mS cm^{-1}.

Marquage

Aux mois de juin et juillet de chaque été, 20 ombles de fontaine de taille adulte (250 à 419 mm de longueur totale) ont été munis d'un radio-émetteur thermosensible. Les poissons ont été capturés à l'aide de filets multifilaments placés perpendiculairement à la rive. L'émetteur a été attaché au niveau de la nageoire dorsale du poisson, après que celui-ci ait été légèrement anesthésié. Quatre poissons ont survécu aux manipulations en 1991, comparativement à 11 en 1992 et à 13 en 1993.

Localisation

Les poissons ont été localisés à tous les deux jours durant chacune des périodes d'échantillonnage. À chacune des visites (8:00 à 18:00), chaque poisson a été localisé et sa position rapportée sur une carte par triangulation à l'aide d'une boussole et de points de repère situés en périphérie du lac. La température ambiante de l'eau mesurée par l'émetteur thermosensible a été relevée à quatre occasions: une première fois lorsque le poisson était localisé (afin d'évaluer sa position verticale en fonction du profil thermique du lac), et à trois autres reprises respectivement au début, au milieu et à la fin de la période de localisation de l'ensemble des individus. Pour chacune des journées d'échantillonnage, la température ambiante de chacun des poissons correspond à la moyenne des quatre mesures. Enfin, à huit reprises entre 1991 et 1993, de cinq à sept individus ont été localisés à tous les quatre heures durant un cycle de 24 heures.

Sélection de sites de fraie

En 1992, les poissons ont été suivis jusqu'à ce qu'ils migrent vers leur site de reproduction, soit trois ruisseaux tributaires du lac Ledoux. La relation entre les préférences spatiales des individus durant l'été et la sélection de sites de fraie a été évaluée.

Analyses statistiques

Nous avons déterminé la zone dans laquelle chaque poisson se situait à chacune des localisations en procédant de la manière suivante: nous avons subdivisé la coupe transversale des lacs en sept zones de taille inégale; une première division en fonction des couches thermiques du lac (épilimnion, métalimnion, et hypolimnion) et une deuxième division de manière à isoler des zones associées au substrat (jusqu'à 1m du fond) et des zones d'eau libre (Fig.1). Les zones 1 et 2 ont été considérées comme "zones benthiques" et les zones 4, 5 et 6 comme "zones pélagiques". Les localisations dans les zones 3 et 7 n'ont pas été considérées dans les analyses puisqu'il a été difficile de les associer à l'une ou l'autre des catégories décrites. Moins de 1% des 486 localisations se situaient dans ces zones. Pour chaque journée d'échantillonnage, la profondeur du poisson, la profondeur du lac à cet endroit, sa température ambiante ainsi que le profil thermique du lac ont été utilisés pour associer les poissons à chacune des zones.

Les variances intra- et interindividuelles au niveau de la température ambiante, obtenues par analyse de variance (ANOVA), ont été comparées afin de déceler des différences intra- et interindividuelles. Aussi, des coefficients de corrélation de Spearman ont été calculés entre certains traits morphologiques (ajustés en fonction de la taille; Packard et Broadman, 1988) et la fréquence des individus en zones benthiques (zones 1 et 2), afin d'identifier une relation avec l'utilisation de l'habitat.

De manière à évaluer quantitativement la relation entre les préférences spatiales des individus et leur patron de coloration, nous avons demandé à cinq personnes de classifier les individus en deux groupes distincts sur la base de la couleur de leur flanc (un groupe "rouge" et un groupe "non-rouge"). Cette classification a ensuite été comparée à celle obtenue à partir des préférences spatiales des individus.

RÉSULTATS

Distribution spatiale

Les poissons ont été arbitrairement classifiés comme individu "benthique" ou "pélagique" lorsqu'ils étaient localisés plus de 60% du temps dans l'une des deux catégories de zone, et en individu "généraliste" lorsqu'ils utilisaient régulièrement les deux habitats. Sur les 28 individus suivis, 14 ont été classifiés comme "benthique", cinq comme "pélagique", et neuf comme "généraliste".

Les poissons étaient plus actifs la nuit (22:00-6:00) que le jour (10:00-18:00) en terme de distance parcourue entre deux localisations consécutives (nuit: 26.2 ± 18.7 m/h; jour: 12.4 ± 15.8 m/h; n = 64).

Sur la base de la fréquence des localisations des individus dans chacun des habitats, les individus benthiques étaient plus fidèles à la zone benthique que les individus pélagiques l'étaient envers la zone pélagique (81.7 ± 9.7 % versus 68.6 ± 4.7%; $F = 81.9$, $p < 0.0001$).

Température ambiante

L'analyse de variance (ANOVA) montre que la variance intra-individuelle au niveau de la température ambiante journalière est beaucoup plus faible que la variance interindividuelle, autant en ce qui concerne l'ensemble des individus que pour chacun des trois groupes pris séparément (Table II).

Caractéristiques morphologiques et patron de coloration

La taille de la nageoire pectorale était corrélée positivement avec la fréquence des individus en zone benthique (Table IV). Suite à la classification des individus en fonction de leur patron de coloration, les quatre individus pélagiques ont été placés dans le groupe "rouge", alors que les 13 individus benthiques et six des sept individus généralistes ont été placés dans le groupe "non-rouge".

Sélection de sites de fraie

À la fin d'octobre 1992, tous les poissons avaient sélectionné un site de reproduction (Figure 3). Les individus pélagiques se sont regroupés dans le ruisseau #2, le seul individu benthique toujours actif a choisi le ruisseau #1, alors que les généralistes se sont dispersés dans les trois ruisseaux. Notons aussi que dans les semaines précédant la sélection des sites de fraie, quatre des neuf poissons se sont déplacés d'un site à l'autre avant d'arrêter leur choix (Fig. 4).

DISCUSSION

Les résultats de cette étude ont permis de montrer qu'il existe des différences interindividuelles dans l'utilisation de l'habitat chez l'Omble de fontaine. Cinquante pour-cent des poissons étaient retrouvés principalement en zone benthique, 18% en zone pélagique, et 32% se déplaçaient de façon régulière entre les deux habitats. La signification écologique de cette ségrégation en trois groupes d'individus de la population est supportée par des variances intra-individuelles au niveau de la température ambiante beaucoup plus faible que les variances interindividuelles. De plus, les poissons ont été suivis durant un minimum de deux mois, sur deux lacs, et durant trois étés. Enfin, sachant que la distribution spatiale des individus détermine la disponibilité des ressources auxquelles ils ont accès, ces différences interindividuelles dans l'utilisation de l'habitat suggèrent des différences interindividuelles au niveau de l'alimentation.

La proportion plus importante d'individus benthiques peut être attribuable à la plus grande profitabilité de l'habitat littoral. On sait que l'Omble de fontaine s'alimente préférablement des organismes benthiques de la zone littorale dans ce système d'étude. Par contre, en sympatrie avec le Meunier noir, *Catostomus commersoni* (Lacépède), l'Omble de fontaine déplace son alimentation sur le zooplancton de la zone pélagique en raison d'une compétition pour les organismes benthiques de la zone littorale avec les meuniers

(Magnan, 1988; Tremblay et Magnan, 1991; Lacasse et Magnan, 1992). Puisque le Meunier noir est absent dans les lacs Ledoux et de l'Epervier, il est possible que plus d'individus choisissent d'exploiter la zone littorale.

Les différences interindividuelles observées au niveau de l'utilisation de l'habitat sont reliées à des différences au niveau de la morphologie, de la coloration, et des préférences thermiques. Les nageoires pectorales des individus benthiques sont significativement plus longues que celles des individus pélagiques. Or, de longues nageoires pectorales sont généralement associées à des mouvements de manoeuvre lents et précis (Gatz, 1979; Webb, 1984), mouvements requis pour une alimentation sur les organismes benthiques retrouvés sur le fond. Inversement, de courtes nageoires pectorales sont associées aux longs déplacements nécessaires à une alimentation efficace en zone pélagique (Ehlinger, 1990).

Comparativement aux individus benthiques et généralistes, le patron de coloration des individus pélagiques est clairement rougeâtre. Chez les poissons, la coloration rouge et principalement due à la présence de pigments de carotène (Brush & Reisman, 1965; Fujii, 1993). Ce pigment ne peut être synthétisé par le poisson et doit donc être absorbé dans l'alimentation (Fujii, 1993). Si la distribution spatiale des individus pélagiques est effectivement corrélée à une alimentation riche en zooplancton, la coloration rouge suggère un important contenu en carotène dans les proies pélagiques.

Les résultats de la présente étude supportent l'hypothèse que des groupes d'individus appartenant à la même espèce (ici les individus benthiques et pélagiques) puissent sélectionner des sites de reproduction différents. Par contre, en raison du faible nombre d'individus suivi jusqu'à période de fraie, d'autre travaux seront nécessaires pour vérifier cette hypothèse.

Quelles soient d'ordre génotypique ou phénotypique, les variations interindividuelles peuvent avoir d'importants effets sur la dynamique des populations. Comme au niveau interspécifique, cette répartition des ressources peut permettre à la population d'atteindre

un niveau plus dense, en plus d'assurer la survie lors de conditions marginales (Morse, 1980). L'étude des mécanismes responsables de la variabilité individuelle au niveau de la morphologie et du comportement, ainsi que la validation des modèles exploitant ces différences phénotypiques entre les individus, vont sûrement compter parmi les plus importantes avenues de recherche en écologie animale dans le futur.

ANNEXE B

Résumé de l'article 2

Structure and determinant of interindividual variation
in the diet of brook charr, *Salvelinus fontinalis*.

INTRODUCTION

L'Omble de fontaine, *Salvelinus fontinalis,* est une espèce carnivore généraliste (Scott et Crossman 1977; Power 1980; Magnan 1988; Lacasse et Magnan 1992) qui a colonisé les lacs du bouclier laurentien suite à la dernière glaciation. Sa morphologie lui permet de se nourrir des deux principales catégories de proies retrouvées dans ces lacs, soit le zoobenthos en zone littorale et le zooplancton en zone pélagique (Tremblay et Magnan 1991, Lacasse et Magnan 1992). Cette espèce représente donc un excellent modèle pour étudier les variations individuelles au niveau de l'alimentation. L'objectif général de la présente étude consiste à identifier la variation interindividuelle dans l'alimentation de l'Omble de fontaine à partir d'une base de données contenant des caractéristiques biotiques et abiotiques de 70 lacs du bouclier canadien. Les objectifs spécifiques sont (1) de décrire la structure des variations interindividuelles dans l'alimentation de l'Omble de fontaine, (2) d'évaluer les déterminants de la spécialisation alimentaire, et (3) d'évaluer le degré de variabilité interindividuelle dans l'alimentation à l'intérieur d'un habitat donné.

MATÉRIEL ET MÉTHODES

Cette étude a été réalisée à partir de l'analyse de contenus stomacaux de 3776 ombles de fontaine issus de 70 lacs des Réserves fauniques Mastigouche (46°40'N, 73°20'O) et Saint-Maurice (45°05'N, 73°15'O). Les données proviennent de sept travaux effectués au cours des dix dernières années par le laboratoire de Pierre Magnan (Magnan 1988; Lachance et Magnan 1990; Tremblay et Magnan 1991; East et Magnan 1991; Lacasse et Magnan 1992; Venne et Magnan 1995; Lapointe et Magnan, données non publiées). Sur l'ensemble des lacs à l'étude, 39 contiennent des populations allopatriques d'Omble de fontaine, 24 contiennent de l'Omble de fontaine et du Mulet à corne, et 16, de l'Omble de fontaine et du Meunier noir.

Une moyenne de 20 estomacs par "unité d'échantillonnage" (définie comme étant un lac donné, pour une date et une taille de poisson données) ont été prélevés sur des ombles de fontaine capturés soit par des pêcheurs sportifs, soit lors de pêches au filet maillant. Le poids des différentes catégories de proies a ensuite été déterminé en laboratoire. Des caractéristiques biotiques et abiotiques des lacs étudiés ont aussi été tirées de certains travaux afin d'être utilisées comme variables indépendantes dans des modèles de régression multiple.

De manière à décrire la structure de la variation interindividuelle, nous avons placé sur un histogramme la fréquence d'individus en fonction du poids des organismes benthiques retrouvés dans leur estomac. Le pourcentage moyen du poids des proies benthiques de chaque unité d'échantillonnage a aussi été mis en relation avec l'écart-type, de manière à quantifier l'importance de la variabilité interindividuelle entre les différentes associations d'espèces (Omble de fontaine seul, Omble de fontaine et Mulet à corne, Omble de fontaine et Meunier noir).

La régression linéaire multiple a été utilisée afin d'estimer les déterminants de la spécialisation alimentaire. Comme variable dépendante, nous avons utilisé le pourcentage d'individus ayant plus de 90% de proies benthiques dans leur estomac, soit les spécialistes benthiques. Un premier modèle a été construit en incluant toutes les unités d'échantillonnage. Ensuite, différents modèles ont été construits pour chacune des études prises séparément, certaines variables indépendantes (physico-chimie, habitat thermique, structure de l'habitat littoral, etc.) étant spécifiques à chacune d'elles. Finalement, afin d'évaluer la variation interindividuelle dans l'alimentation à l'intérieur d'un même habitat, nous avons comparé, pour des spécialistes benthiques appartenant à une même unité d'échantillonnage, la fréquence de huit catégories de proies benthiques dans leur estomac.

RÉSULTATS ET DISCUSSION

Variation interindividuelle dans l'alimentation de l'Omble de fontaine

Les résultats de la présente étude ont permis de montrer qu'il existe des variations interindividuelles dans l'alimentation de l'Omble de fontaine. En effet, dans une même population, alors que certains individus se nourrissent presqu'exclusivement d'organismes benthiques, certains autres s'alimentent presqu'exclusivement d'organismes zooplanctoniques. Ainsi, l'espèce ne semble pas composée d'un ensemble d'individus généralistes, en terme d'alimentation, mais surtout par des spécialistes de chacune des catégories de proies ("benthophages" et zooplanctonophages").

Ces résultats supportent les conclusions de Bourke *et al.* (article 1). En effet, dans cette étude, on a montré que sur la base de leur distribution spatiale, les ombles de fontaine peuvent être subdivisés en deux groupes de spécialistes (littoraux et pélagiques) et un groupe de généralistes. De plus, les différences interindividuelles observées dans la sélection de l'habitat étaient reliées à des différences au niveau de la morphologie de la nageoire pectorale et de la coloration, deux caractéristiques apparemment liées à l'alimentation.

L'analyse des contenus stomacaux montre aussi d'importantes différences au niveau de la variation interindividuelle entre les communautés de poissons. En effet, la proportion d'individus spécialistes du benthos décroît de 41.3% en allopatrie, à 19.7% en sympatrie avec le Mulet à corne, et enfin à 9.9% en sympatrie avec le Meunier noir. On remarque aussi que la proportion de généralistes est relativement faible et demeure sensiblement la même entre les communautés, suggérant que les déplacements de niche alimentaire s'effectuent au niveau des spécialistes. Enfin, ces résultats confirment les conclusions de Magnan (1988) et de Lacasse et Magnan (1992) concernant l'impact plus important qu'a le Meunier noir sur le changement de niche de l'Omble de fontaine.

Déterminants de la spécialisation

Les différents modèles de régression multiple ont permis de faire ressortir un certain nombre de déterminants de la spécialisation alimentaire chez l'Omble de fontaine. Les plus importants sont la présence du Meunier noir (-), les profondeurs maximale et moyenne des lacs (-), le mois (mai à septembre) (-), ainsi que la présence du Mulet à corne (-). Toutes ces variables ont un impact plus ou moins important sur l'abondance de la ressource benthique. Par conséquent, la disponibilité des proies benthiques semble avoir une grande influence sur l'importance de la variabilité individuelle dans l'alimentation chez l'Omble de fontaine (i.e. sur la proportion de chacun des deux groupes: "benthonophages" et "zooplanctonophages").

Variabilité intra-habitat

Les résultats de cette étude nous ont aussi permis de montrer qu'il existe des variations individuelles dans l'alimentation des spécialistes des proies benthiques. Par exemple, les larves d'Ephéméroptères comptent pour la grande majorité des proies retrouvées dans l'estomac de neuf des dix individus capturés dans la zone littorale du lac Vautour, le 19 juin 1985. Toutefois, alors que les éphéméroptères représentent plus de 80% de l'alimentation de certains individus, elles sont absentes ou comptent pour moins de 30% de l'alimentation chez d'autres individus. De telles différences ont aussi été observées dans le cas des sept autres catégories de proies. Il est cependant difficile d'affirmer si ces différences sont reliées à des préférences alimentaires, à l'efficacité d'alimentation, ou si l'on assiste simplement à une conséquence de la distribution hétérogène des proies dans l'habitat littoral. Seule des données provenant de l'alimentation de mêmes individus à différentes périodes permettraient de mieux répondre à ces questions.

ANNEXE C

Résumé de l'article 3

Diel locomotor activity of brook charr,
Salvelinus fontinalis, as determined by radio-telemetry

INTRODUCTION

Les salmonidés sont généralement considérés comme des poissons diurnes (voir Linner *et al.*, 1990). Toutefois, nos observations préliminaires suggèrent un patron d'activité nocturne chez l'Omble de fontaine adulte en lac. Bien que les patrons d'activité aient été souvent étudiés chez les ombles vivant en milieu lotique, bien peu de travaux se sont penché sur les populations lacustres. Les objectifs de cette étude sont (1) d'évaluer le patron d'activité locomoteur de l'Omble de fontaine adulte en lac en utilisant la radio-télémétrie, (2) de comparer ces résultats avec ceux obtenus par des captures au filet maillant, et (3) de comparer le patron d'activité des adultes à celui des jeunes de l'année et des juvéniles.

Cette étude a été menée dans les lacs de L'Épervier, Ledoux, Simpson, et Bondi situés dans la Réserve faunique Mastigouche (46°40'N, 73°20'O), ainsi qu'au lac Melchior, dans la Réserve faunique Saint-Maurice (45°05'N, 73°15'O). Ces lacs sont représentatifs des petits lacs oligotrophes de la zone tempérée.

MATÉRIEL ET MÉTHODES

Marquage

Au mois de juin et juillet de chaque été, 20 ombles de fontaine de taille adulte (250 à 419 mm de longueur totale) ont été munis d'un radio-émetteur thermosensible. Les poissons ont été capturés à l'aide de filets multifilaments placés perpendiculairement à la rive. L'émetteur était attaché au niveau de la nageoire dorsale du poisson, après que celui-ci ait été légèrement anesthésié. Quatre poissons ont survécu aux manipulations en 1991, comparativement à 11 en 1992 et à 13 en 1993.

Localisation

Les poissons ont été localisés à tous les deux jours durant chacune des périodes d'échantillonnage. À chacune des visites (8:00 à 18:00), chaque poisson a été localisé et sa position rapportée sur une carte par triangulation à l'aide d'une boussole et de points de repère situés en périphérie du lac. La température ambiante de l'eau mesurée par l'émetteur thermosensible a été relevée à quatre occasions: une première fois lorsque le poisson est localisé (afin d'évaluer sa position verticale en fonction du profil thermique du lac), ainsi qu'à trois autres reprises respectivement au début, au milieu et à la fin de la période de localisation de l'ensemble des individus. Pour chacune des journées d'échantillonnage, la température ambiante de chacun des poissons correspond à la moyenne des quatre mesures.

À deux occasions en 1991 et à trois reprises en 1992 et 1993, les poissons ont été localisés à tous les quatre heures durant un cycle de 24 heures. Ainsi, à chacun des cycles, de cinq à sept individus ont été localisés à 10h, 14h, 18h, 22h, 2h, et 6h de manière à évaluer leur patron d'activité locomoteur.

Pêche au filet

Afin d'évaluer le patron d'activité locomoteur journalier de l'Omble de fontaine adulte (2+, 3+) sur la base de captures au filet maillant, deux stations d'échantillonnage ont été établies au Lac Melchior. Une première située en zone littorale et une autre en zone pélagique (6-8 m de profondeur). À trois reprises en 1979 (Juin, Juillet, et Août), le total des captures a été relevé à tous les quatre heures durant un cycle de 24 heures.

À partir de données provenant de deux autres études (Dynes et Magnan; Héroux et Magnan) nous avons pu étudier l'activité locomotrice journalière des jeunes de l'année (0+) et des juvéniles (1+) respectivement. Au lac Simpson, des ombles juvéniles (106 à 188 mm) ont été capturés à trois heures d'intervalle durant un cycle de 48 heures. Au lac Bondi, des jeunes de l'année (60.0 ± 4.5 mm) ont aussi été capturés en zone littorale à 8h,

12h, 16h, et 20h. Les filets ont été placés perpendiculairement à la rive en huit stations autour du lac.

Analyses statistiques

Afin d'évaluer le patron d'activité locomoteur journalier des ombles adultes à partir de la radio-télémétrie, deux mesures différentes de déplacement ont été calculées. Premièrement, la "distance minimale parcourue" représentant la distance linéaire (m) entre deux localisations consécutives. Cinq mesures de "distance minimale" ont donc été obtenues pour chaque poisson, soit une pour chacun des intervalles du cycle (i.e. 10-14h, 14-18h, 18-22h, 22-2h et 2-6h).

Les localisations journalières ont démontré que les poissons sont relativement fidèles à un site particulier entre 8:00 et 18:00. Ainsi, il a été possible de calculer pour chaque poisson un "point focal" correspondant au point central de l'ensemble de ses localisations le jour. La distance moyenne de chaque individu par rapport à son point focal a été comparée entre les différentes périodes du cycle. De cette manière, la "distance minimale parcourue" fournie des informations sur l'importance des mouvements entre deux localisations consécutives, sans aucune référence à l'espace, alors que la "distance du point focal" décrit les déplacements dans l'espace en fonction des périodes du jour.

Afin d'évaluer quantitativement le patron d'activité locomoteur journalier de l'Omble de fontaine sur la base des pêches au filet maillant, nous avons construit des distributions de fréquence de captures en fonction des différentes périodes du jour, pour chacun des cycles effectués aux lacs Melchior, Simpson et Bondi.

RÉSULTATS

Sur la base de la "distance minimale parcourue" entre deux localisations consécutives, les ombles adultes sont plus actifs le soir et la nuit comparativement au jour (Table III). Durant le jour, les individus démontrent une forte sélection de site, demeurant

relativement autour du même site d'une journée à l'autre (Table IV). De plus, ces sites sont localisés dans la même partie du lac pour tous les individus (Figure 1).

Au niveau des captures au filet, les jeunes de l'année (0+) sont surtout actifs entre 10:00 et 18:00h (Figure 4, A), alors que les juvéniles (1+) sont actifs durant toute la durée du cycle (Figure 4, B). Enfin, tel qu'on a pu l'observer avec la télémétrie, les fréquences de captures au lac Melchior suggèrent une activité locomotrice plus importante le soir et la nuit chez l'adulte (Figure 4, C).

DISCUSSION

Activité locomotrice journalière chez l'adulte

Les présents résultats suggèrent que durant une période de 24 heures, la distribution et l'activité locomotrice des ombles de fontaine adultes en lacs se subdivisent en deux phases distinctes, l'une diurne, l'autre nocturne. Durant le jour, les ombles sont moins actifs comparativement au soir et à la nuit. De plus, le soir et la nuit, on retrouve les poissons à des distances plus importantes de leur point focal comparativement au jour. Enfin, les captures au filet maillant au lac Melchior supportent ce patron d'activité locomoteur.

Certaines évidences suggèrent que ce patron d'activité puisse refléter le patron d'alimentation de l'Omble de fontaine. Premièrement, les ombles adultes devraient s'alimenter plus activement la nuit afin de profiter de la plus grande disponibilité des proies benthiques (Grossman *et al.*, 1980). Deuxièmement, dans une étude de Naud et Magnan (1987), on remarque que le Ventre rouge du nord, une espèce présente dans les lacs Ledoux et de l'Épervier, effectue des migrations journalières entre la zone littorale et la zone pélagique. Ce patron de déplacement est presqu'identique à celui des ombles de fontaine de la présente étude (Figure 5). Or, selon East et Magnan (1991), la prédation sur cette espèce peut représenter jusqu'à 30% de la diète de l'Omble de fontaine adulte.

La concentration des points focaux de l'ensemble des individus dans la même partie du lac pourrait être expliquée en partie par les contraintes thermiques de l'Omble de fontaine. En fait, la pente du lac est très abrupte dans ce secteur du lac (~ 45°). En raison de la stratification thermique, ceci pourrait permettre aux individus de réduire leurs déplacements horizontaux entre l'aire d'alimentation (en zone littorale) et un refuge thermique situé plus bas dans la colonne d'eau.

Changement ontogénique au niveau de l'activité locomotrice

De récentes études sur les jeunes de l'année d'Omble de fontaine (0+) en lac (Boisclair, 1992) et sur les jeunes de l'année et les juvéniles (1+) en ruisseau (Hoar, 1942; Allan, 1981; Walsh *et al.*, 1988; Forrester *et al.*, 1994) démontrent que ceux-ci sont surtout actifs le jour. Suite aux captures effectuées au lac Bondi, les jeunes de l'année semblent aussi plus actifs le jour. D'autre part, l'activité locomotrice journalière des juvéniles (1+) du lac Simpson démontre une activité aussi intense le jour que la nuit. Cette activité diurne se démarque du patron d'activité des adultes (2+, 3+) et suggère la présence de changement ontogénique de l'activité locomotrice chez l'Omble de fontaine.

Deux hypothèses ont été avancées jusqu'ici pour expliquer de telles différences ontogéniques: l'efficacité alimentaire et l'évitement de la prédation. Pour des raisons d'ordres anatomique et physiologique, les jeunes poissons sont moins efficaces pour s'alimenter à faible intensité lumineuse puisque leurs yeux captent moins de lumière comparativement à ceux des plus grands individus (Helfman, 1979). De plus, à mesure que le poisson croît, la taille de la bouche augmente, permettant aux grands poissons de se nourrir de proies plus grosses, souvent plus actives la nuit (Helfman, 1986).

Le changement ontogénique observé pourrait aussi être le résultat d'une stratégie d'anti-prédateur. En effet, alors que les gros poissons sont plus actifs la nuit, les petits individus peuvent réduire le risque d'être mangés en changeant d'habitat, en réduisant leur taux d'alimentation, leurs mouvements, ou encore en modifiant leur patron d'activité

(Turner & Mittlebach, 1990).

ANNEXE D

Pourcentage moyen du poids des huit catégories
de proies benthiques identifiées par Tremblay et Magnan (1991).
Les données sont présentées uniquement pour les poissons ayant plus de 90%
de benthos dans leur estomac.

Tableau 1. Pourcentages moyens du poids des huit catégories de proies benthiques retrouvées dans l'estomac de six individus (ayant plus de 90% de benthos dans leur estomac) capturés le 26 mai 1985 au Lac Vautour (Tremblay et Magnan 1991).

No	Dipt.	Trichop	Ephem.	Odon.	Chiro.	Sial.	Gamm.	Autre
1	0.40	0.00	87.80	10.72	1.08	0.00	0.00	0.00
2	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00
3	0.71	12.73	58.41	27.13	1.01	0.00	0.00	0.00
4	0.00	0.00	13.70	83.15	3.15	0.00	0.00	0.00
5	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00
6	3.35	0.00	75.65	21.00	0.00	0.00	0.00	0.00

Tableau 2. Pourcentages moyens du poids des huit catégories de proies benthiques retrouvées dans l'estomac de six individus (ayant plus de 90% de benthos dans leur estomac) capturés le 12 juillet 1985 au Lac Vautour (Tremblay et Magnan 1991).

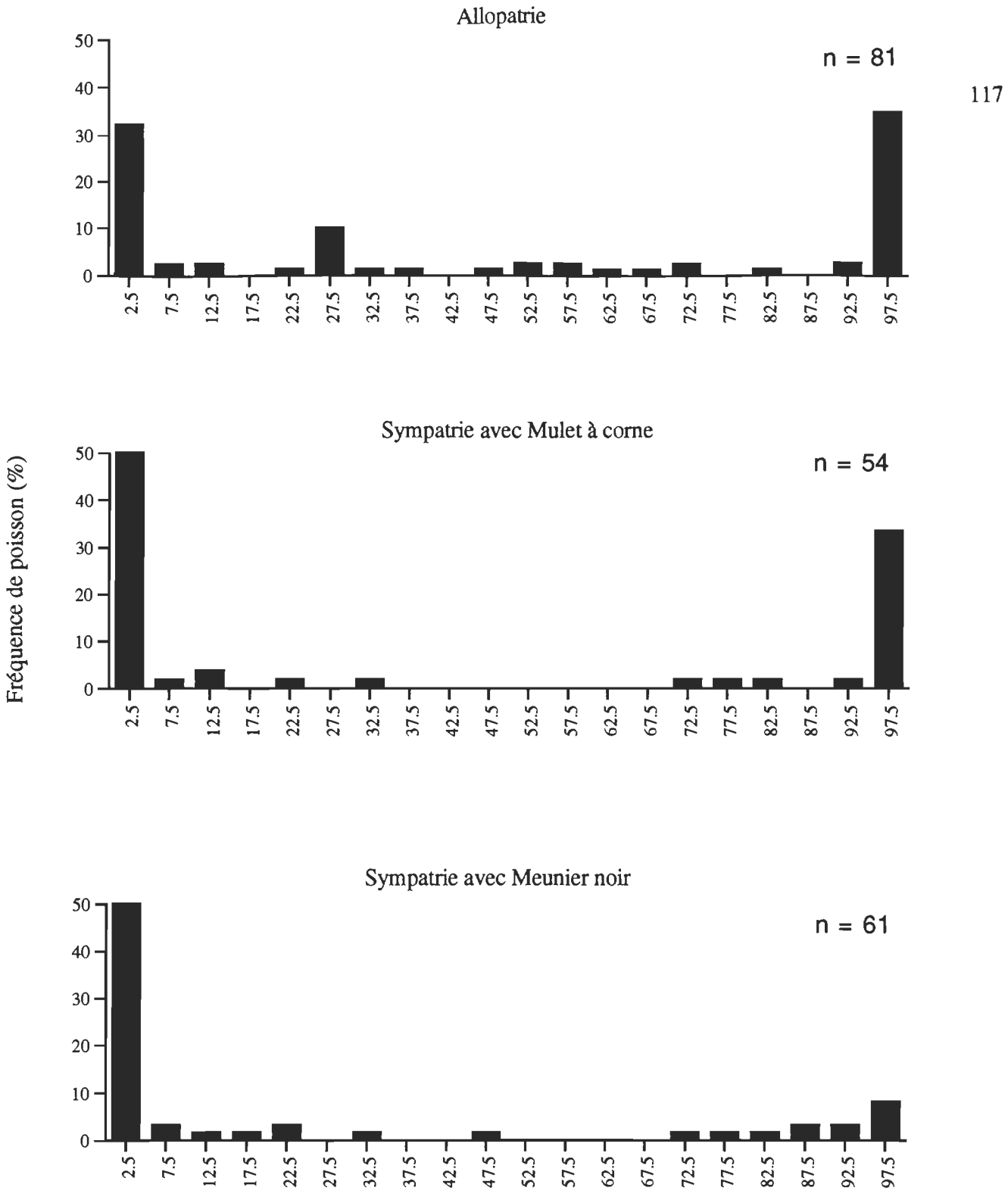
No	Dipt.	Trichop.	Ephem.	Odon.	Chiro.	Sial.	Gamm.	Autre
1	0.00	5.84	18.02	1.84	0.00	74.30	0.00	0.00
2	0.00	0.00	62.69	10.24	3.81	23.26	0.00	0.00
3	0.00	3.54	80.16	4.21	0.00	12.09	0.00	0.00
4	0.00	0.00	33.79	9.58	0.00	56.38	0.00	0.26
5	0.00	0.00	82.59	6.67	0.00	10.74	0.00	0.00
6	0.00	0.00	20.34	39.66	0.00	40.01	0.00	0.00

Tableau 3. Pourcentages moyens du poids des huit catégories de proies benthiques retrouvées dans l'estomac de sept individus (ayant plus de 90% de benthos dans leur estomac) capturés le 9 août 1985 au Lac Vautour (Tremblay et Magnan 1991).

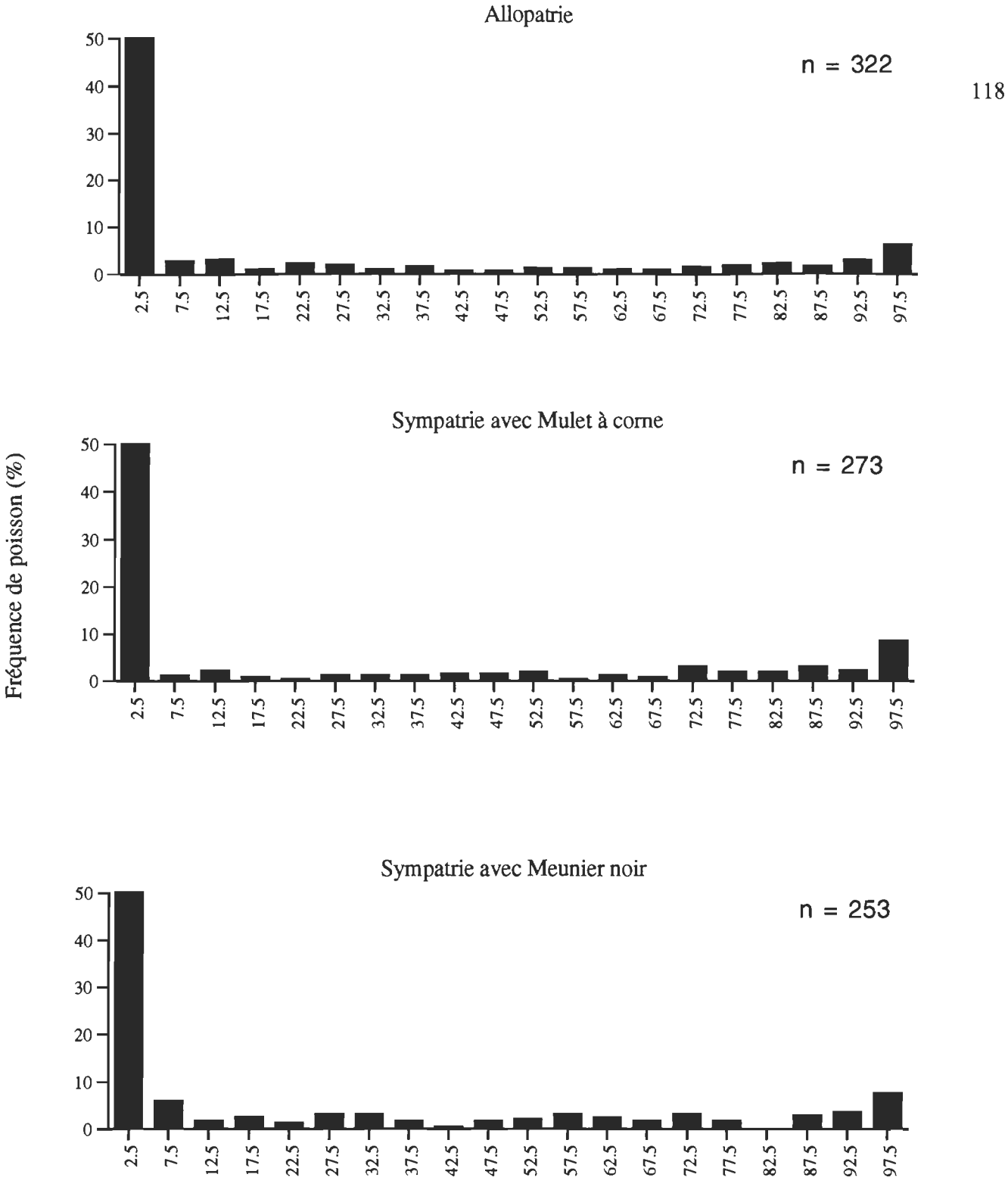
No	Dipt.	Trichop.	Ephem.	Odon.	Chiro.	Sial.	Gamm.	Autre
1	0.00	0.00	90.00	10.00	0.00	0.00	0.00	0.00
2	0.00	0.00	22.31	25.18	0.00	52.50	0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	10.93	0.00	89.07
4	0.00	0.00	61.53	38.47	0.00	0.00	0.00	0.00
5	0.00	0.00	76.13	12.77	0.00	10.45	0.65	0.00
6	0.00	0.00	24.77	24.95	0.00	23.01	0.00	27.27
7	0.66	0.00	36.96	37.61	0.00	23.27	1.50	0.00

ANNEXE E

Distributions de fréquence des individus en fonction du pourcentage de proies benthiques dans leur estomac.

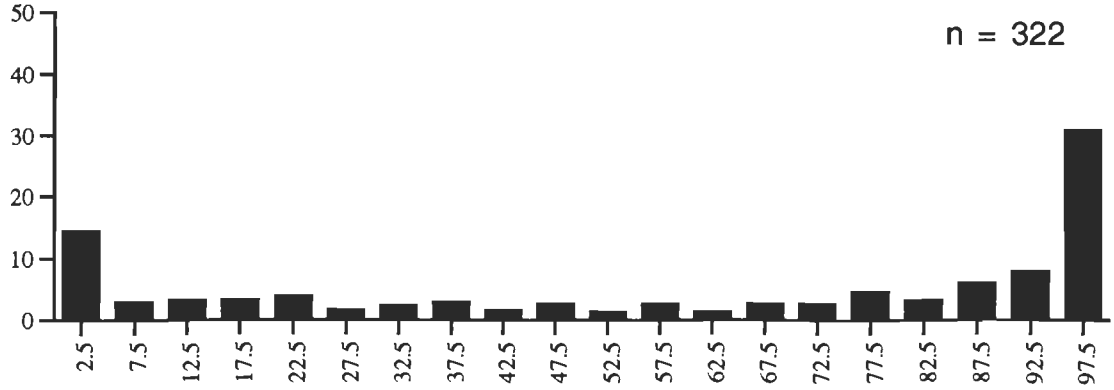


Pourcentage moyen du poids des proies benthiques (%)
(Magnan, 1988)



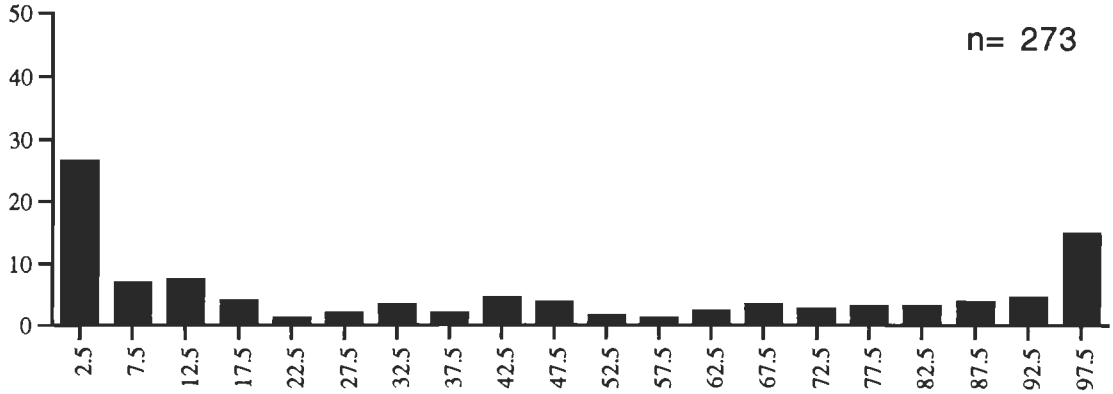
(Lacasse et Magnan, 1992)

Allopatrie

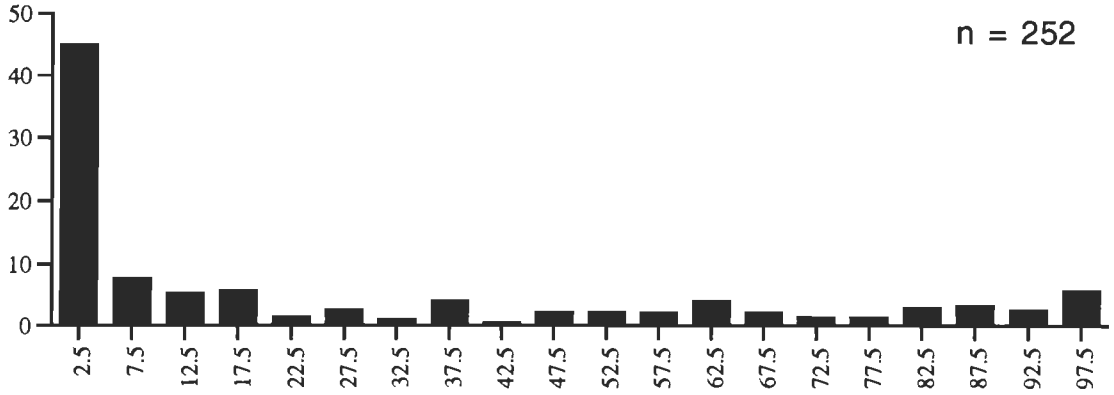


Sympatrie avec Mulet à corne

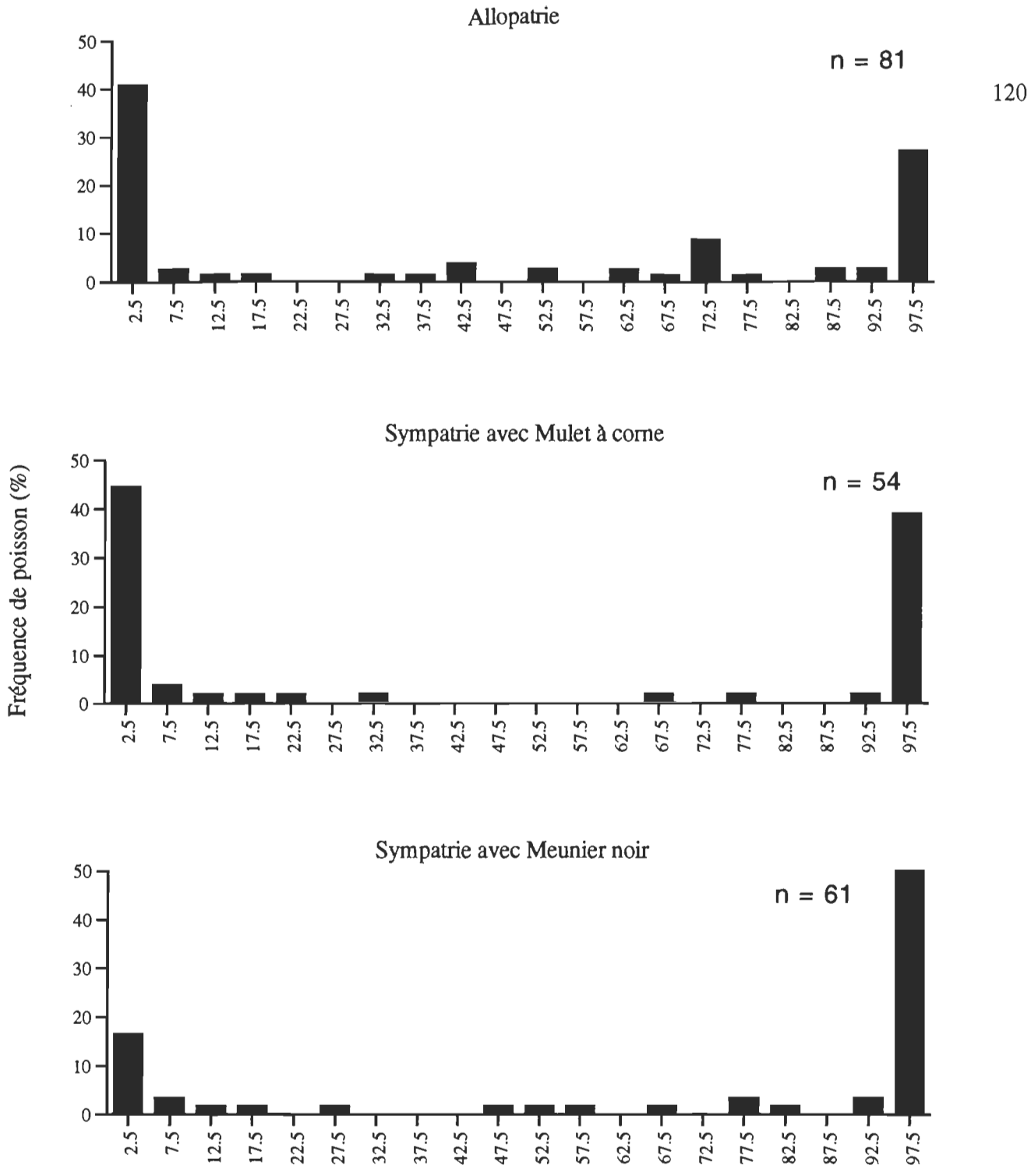
Fréquence de poisson (%)



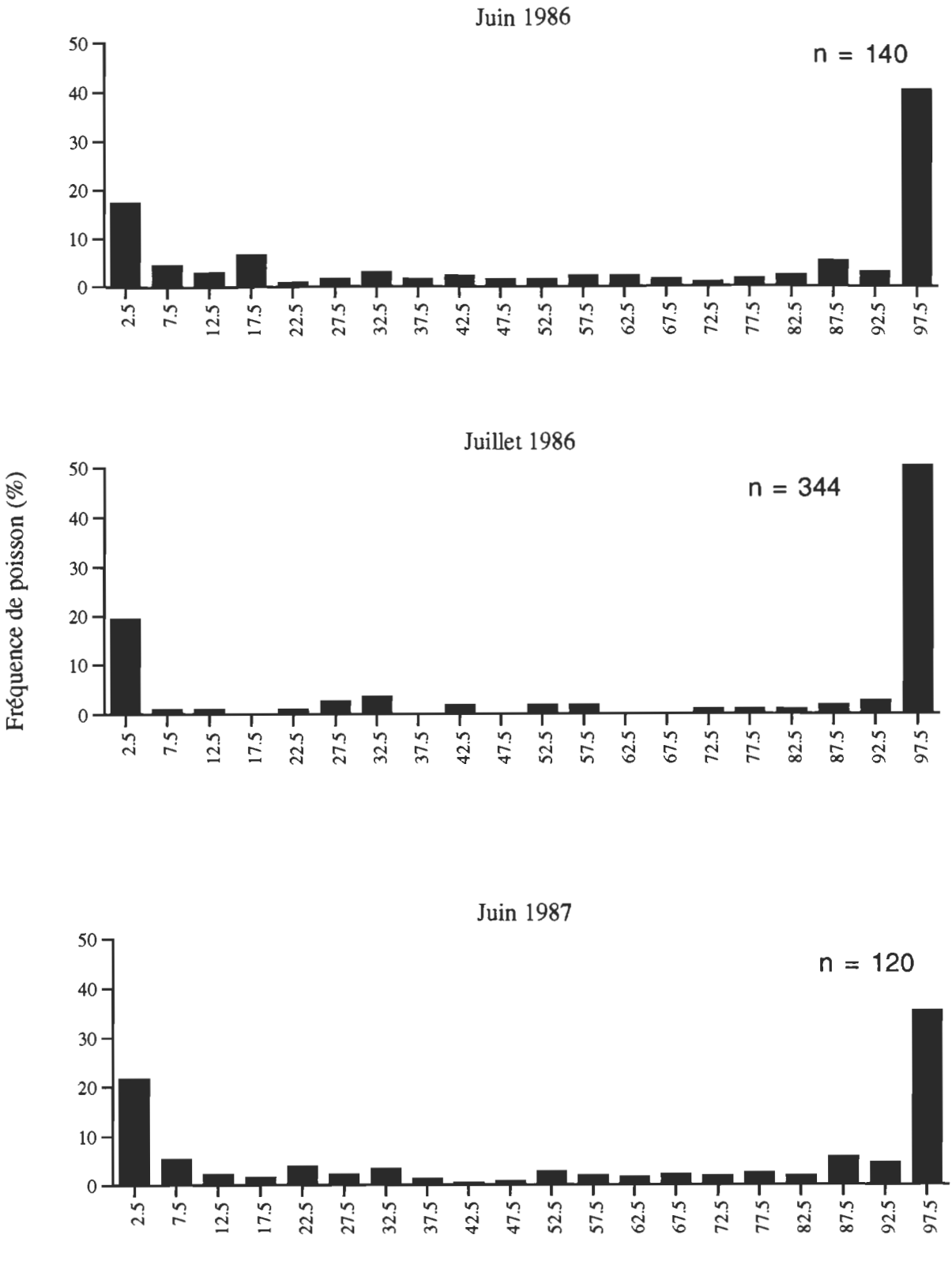
Sympatrie avec Meunier noir



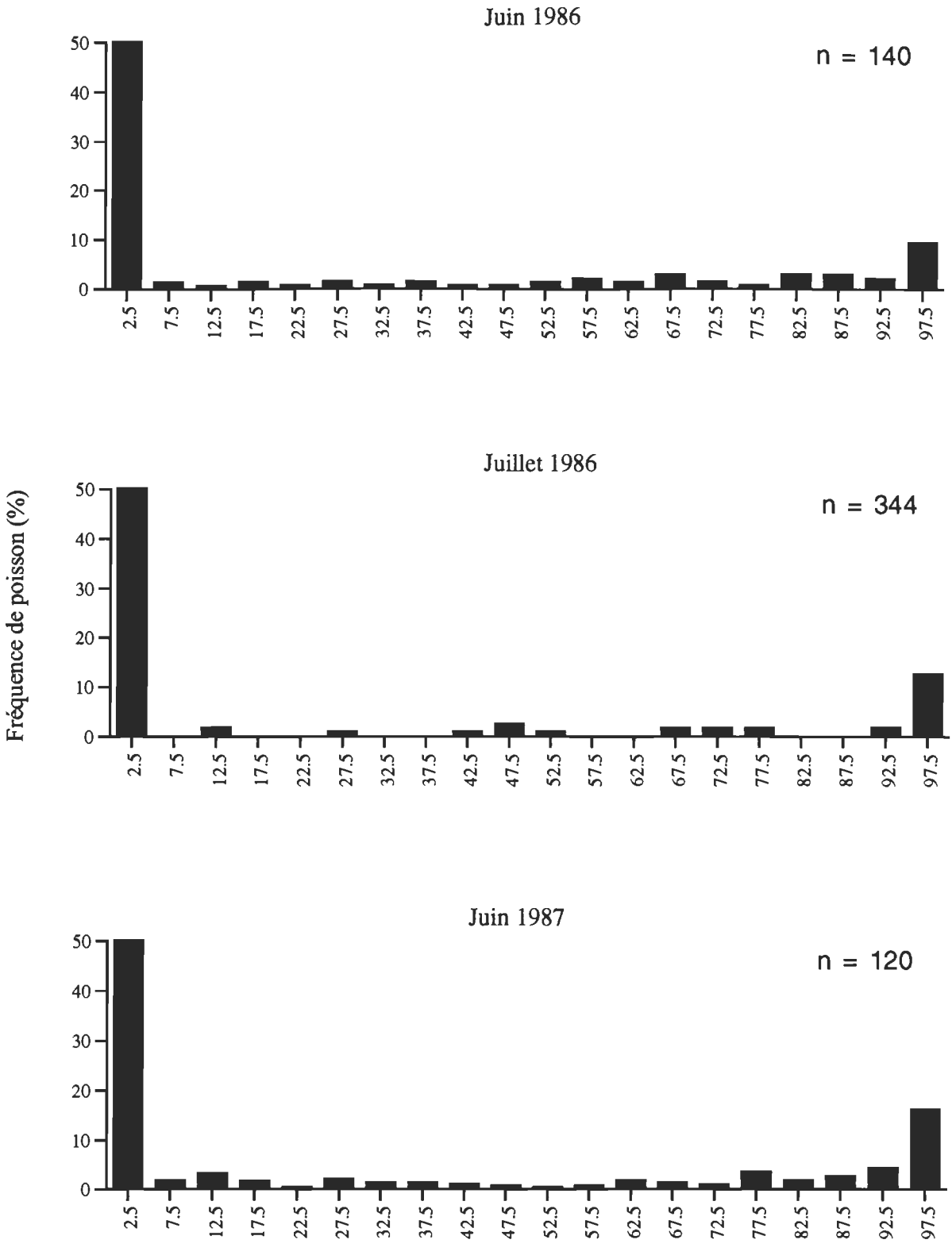
Pourcentage moyen du poids des proies benthiques (%)
(Lacasse et Magnan, 1992)



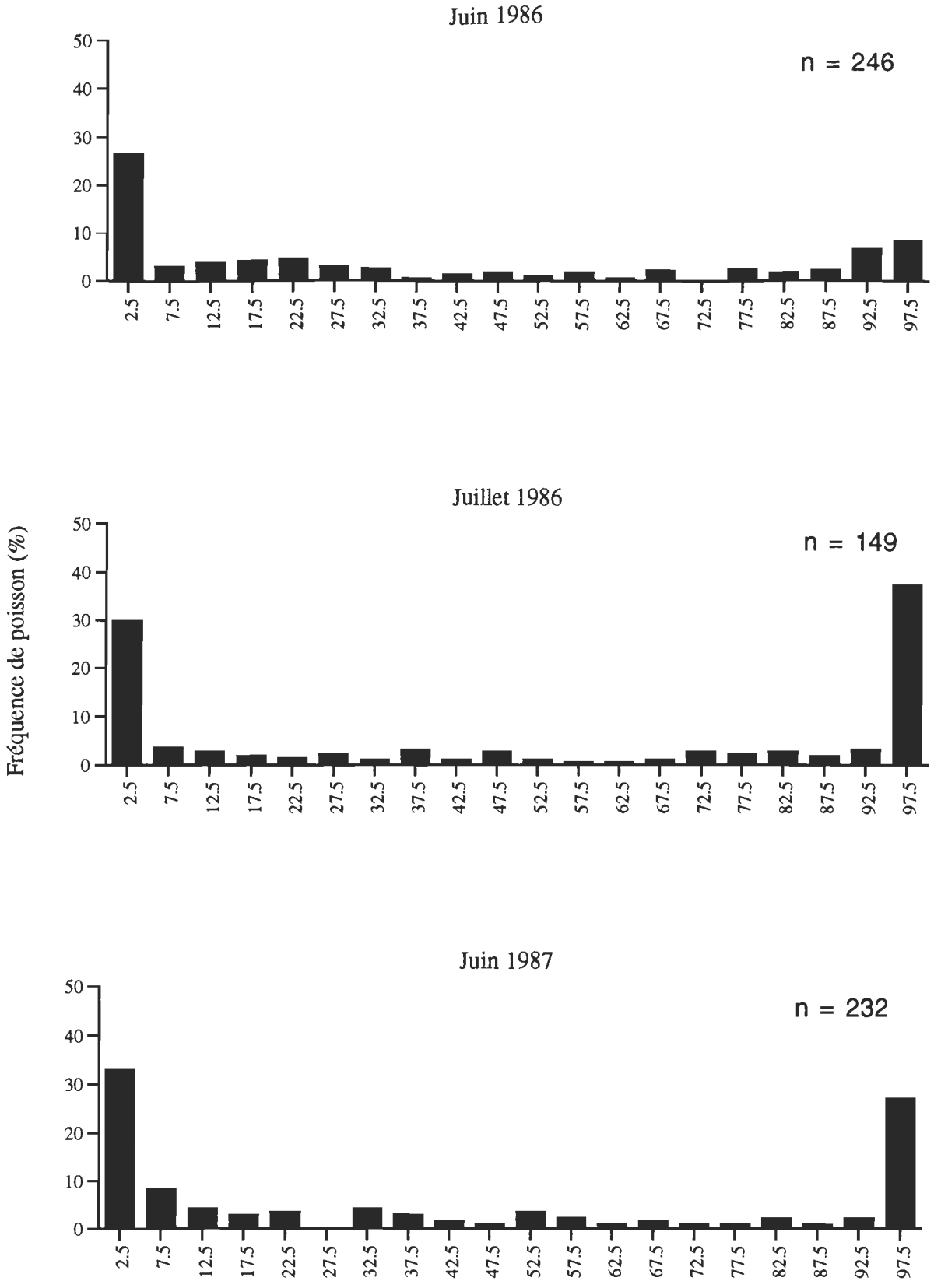
Pourcentage moyen du poids des proies zooplanctoniques (%)
(Magnan, 1988)



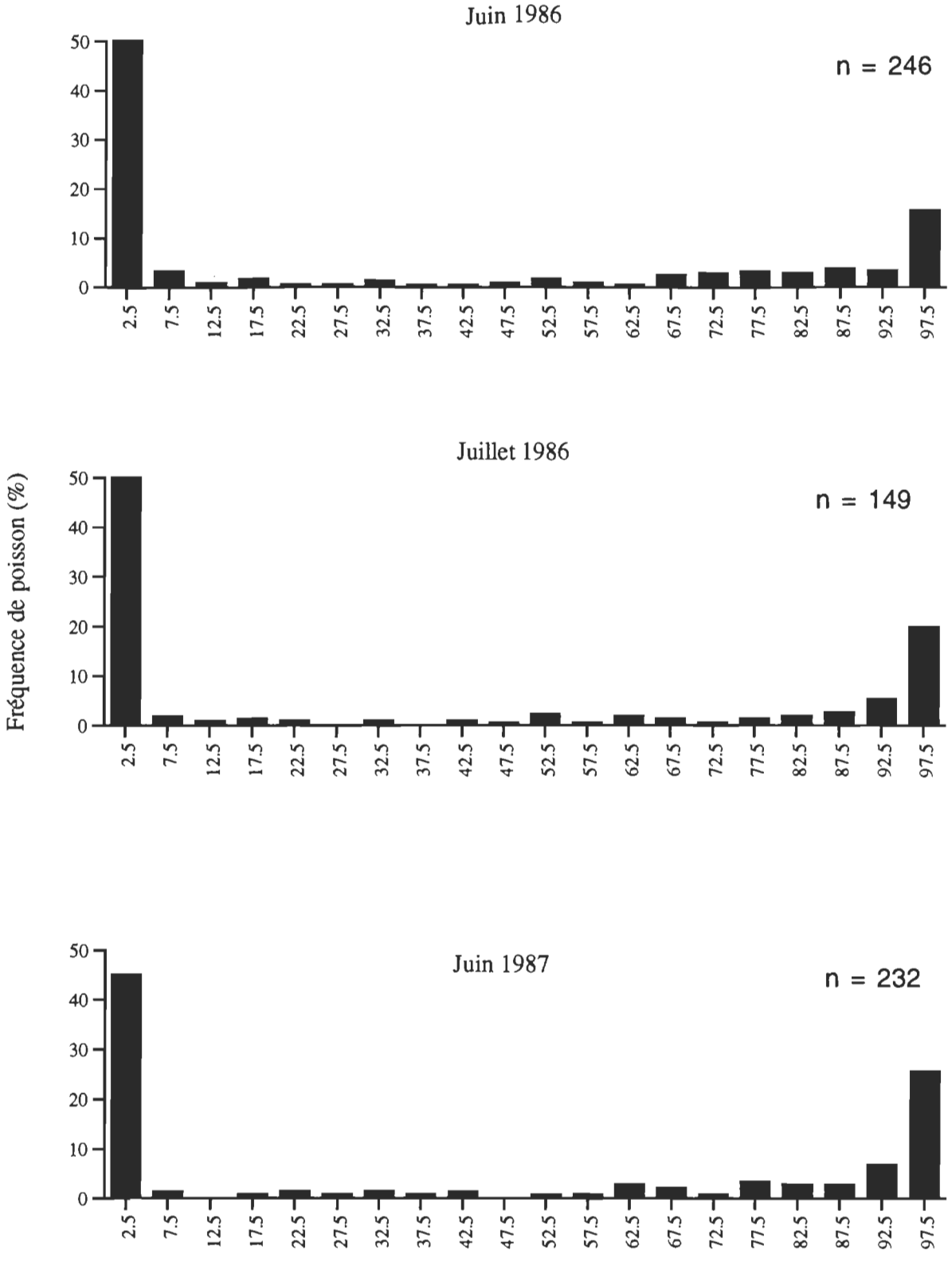
Pourcentage moyen du poids des proies benthiques dans les lacs allopatriques (%) (East et Magnan, 1991)



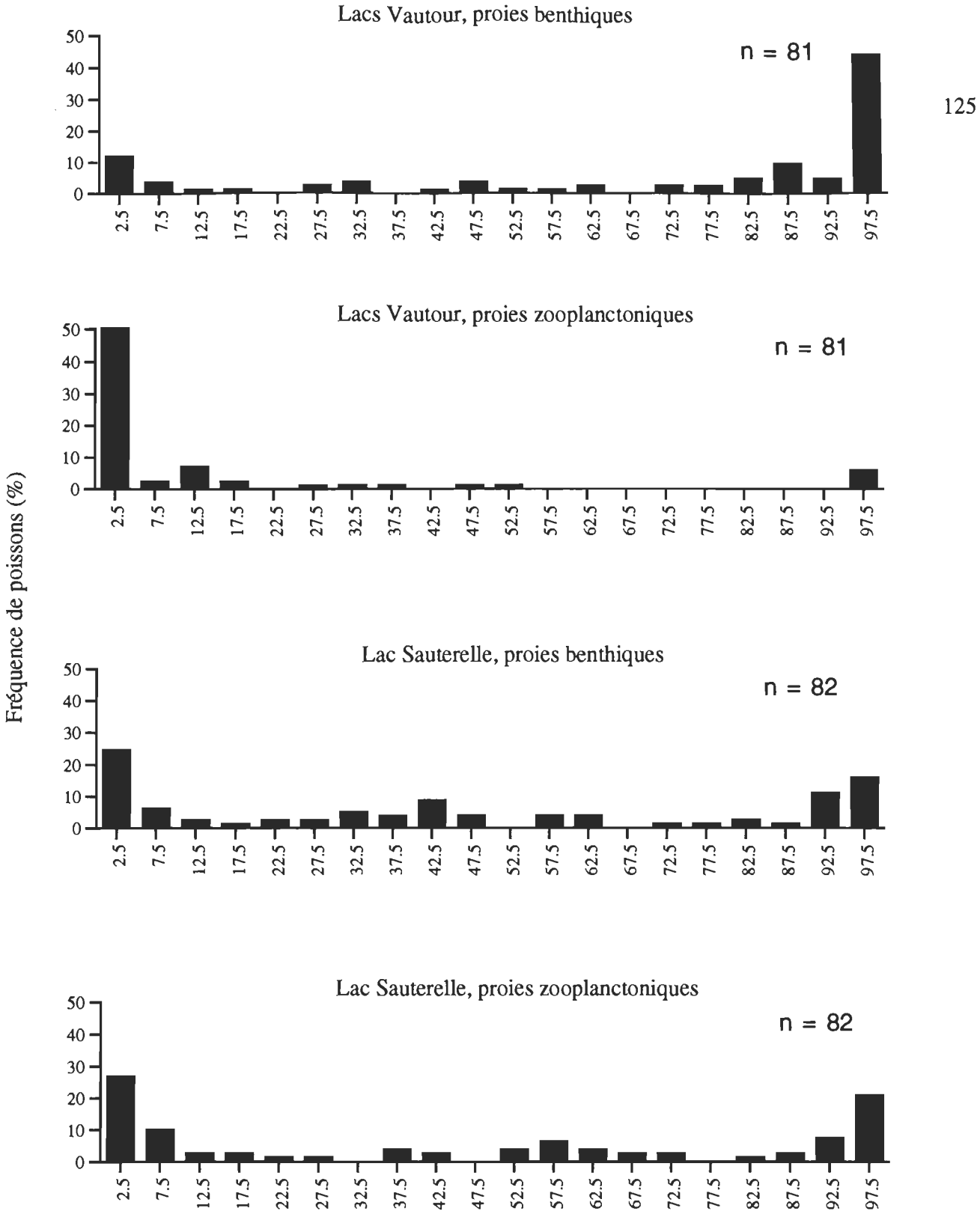
Pourcentage moyen du poids des proies zooplanctoniques dans les lacs allopatriques (%) (East et Magnan, 1991)

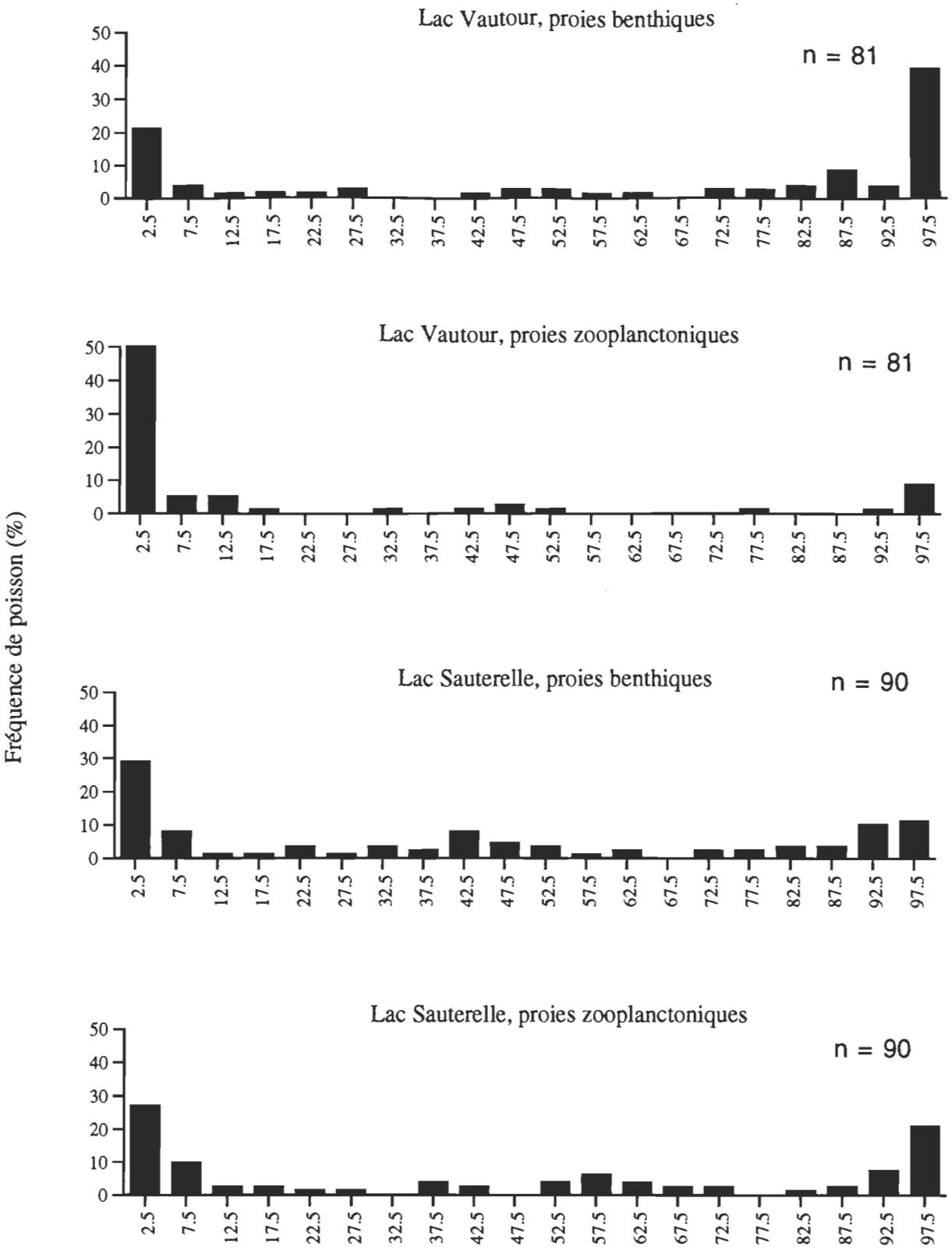


Pourcentage moyen du poids des proies benthiques
dans les lacs à Mulet à corne (%) (East et Magnan, 1991)

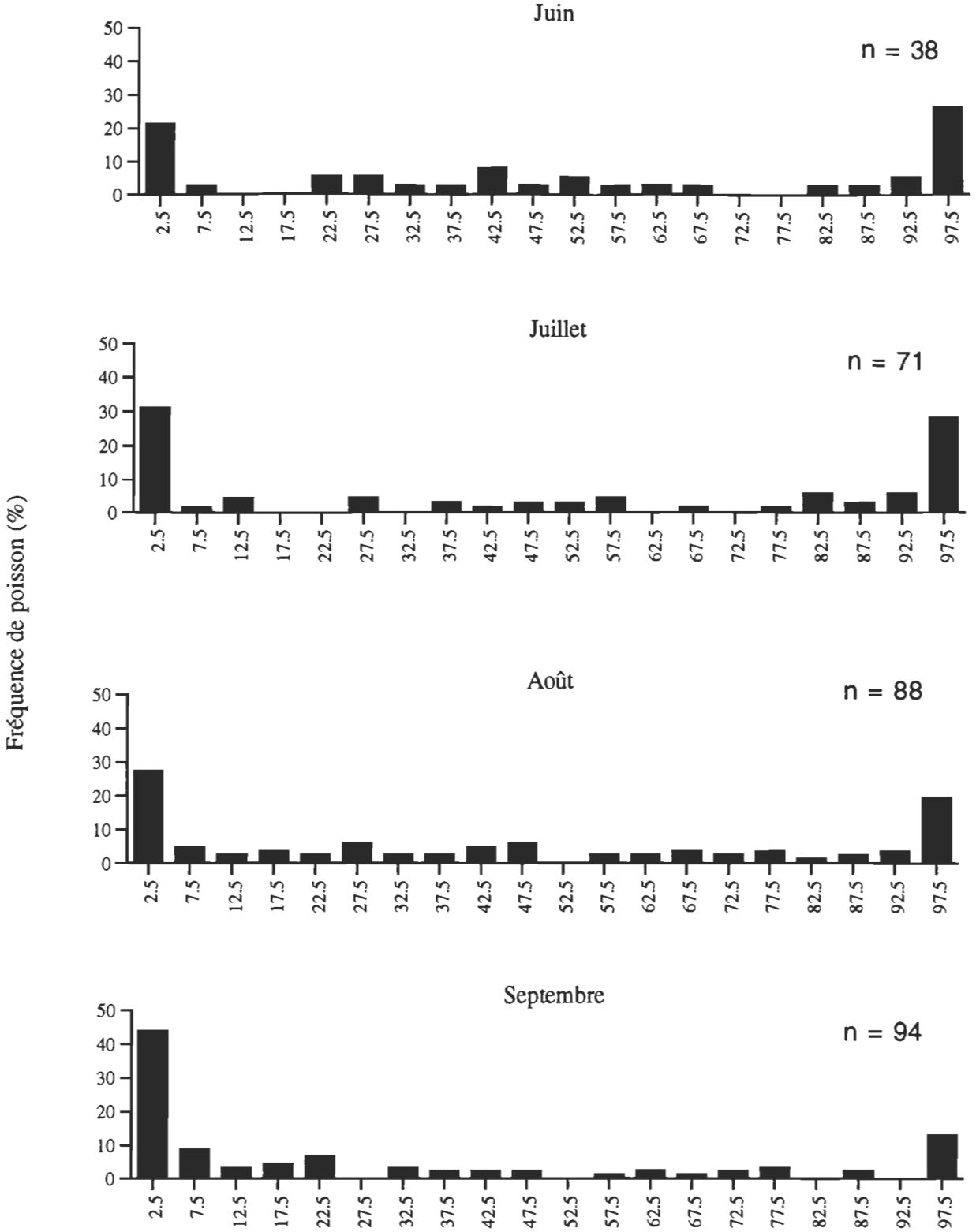


Pourcentage moyen du poids des proies zooplanctoniques dans les lacs à Mulet à corne (%) (East et Magnan, 1991)

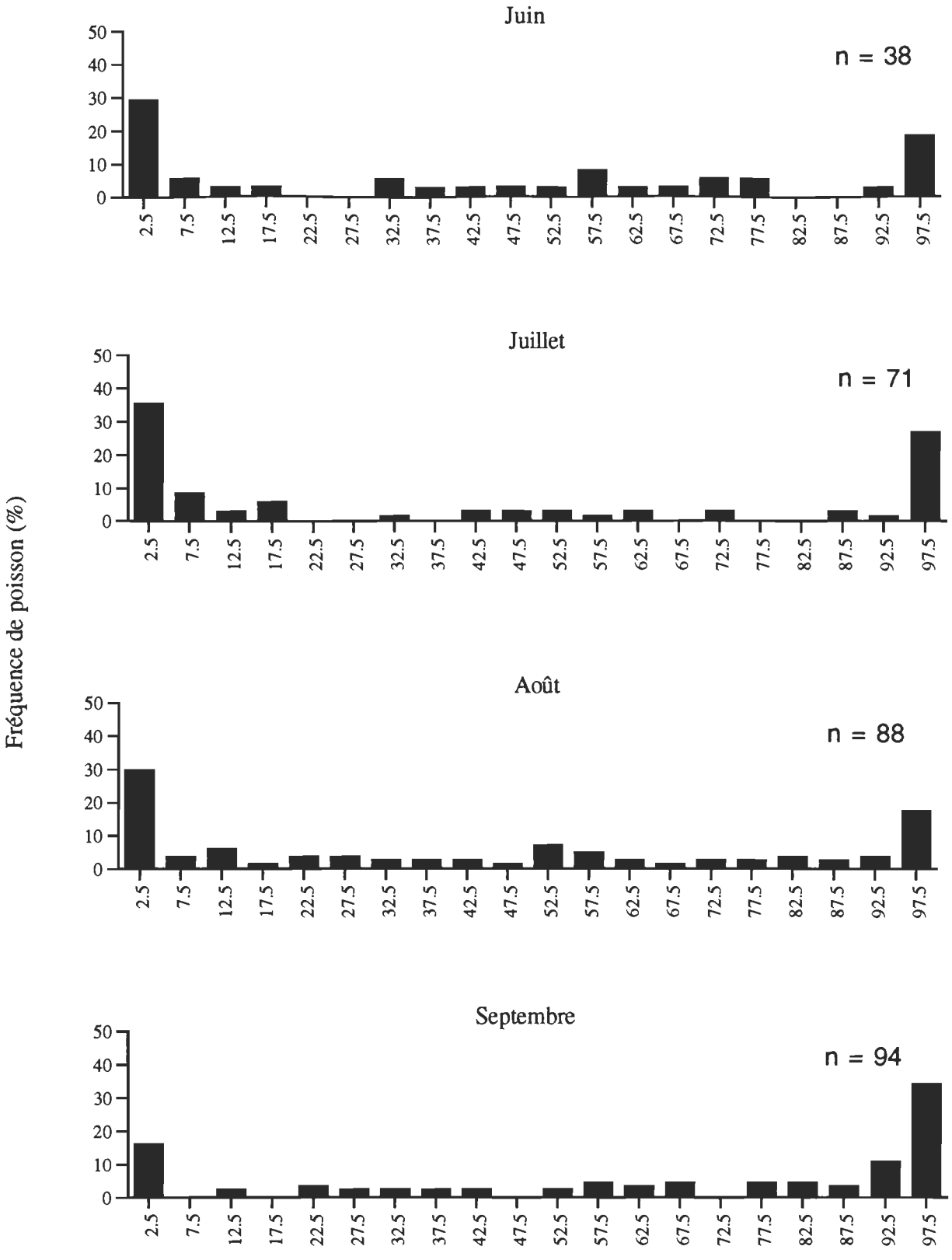

Lacs Vautour, proies benthiques
n = 81
Lacs Vautour, proies zooplanctoniques
n = 81
Lac Sauterelle, proies benthiques
n = 82
Lac Sauterelle, proies zooplanctoniques
n = 82
Fréquence de poissons (%)
0
10
20
30
40
50
2.5
7.5
12.5
17.5
22.5
27.5
32.5
37.5
42.5
47.5
52.5
57.5
62.5
67.5
72.5
77.5
82.5
87.5
92.5
97.5
Pourcentage moyen du poids des proies pour les poissons capturés en zone littorale (%) (Tremblay et Magnan, 1991)



Pourcentage moyen du poids des proies pour les poissons capturés en zone pélagique (%) (Tremblay et Magnan, 1991)



Pourcentage moyen du poids des proies benthiques (%)
(Venne et Magnan, 1995)



Pourcentage moyen du poids des proies zooplanctoniques (%)
(Venne et Magnan, 1995)